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Systematic review of *Pseudobarbus burchelli* (Teleostei, Cyprinidae), with revalidation of *P. vulneratus* and description of a new species

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Abstract

Pseudobarbus burchelli (Smith, 1841) was previously considered to have a relatively wide distribution range spanning four isolated river systems in the Cape Fold Ecoregion of South Africa: the Breede, Duiwenhoks, Goukou, and Heuningnes. Extensive exploration and the application of molecular data led to the discovery and description of a new species, *Pseudobarbus skeltoni*, from the Breede River system, and the identification of three distinct lineages within *P. burchelli*. These lineages were provisionally named *P. burchelli* 'Tradouw' from the Tradouw catchment in the Breede River system, *P. burchelli* 'Breede', distributed across the Breede, Duiwenhoks, and Goukou river systems, and *P. burchelli* 'Heuningnes', distributed in the Heuningnes River system. Additionally, recent surveys found a new redfin population in the upper Klein River, genetically linked to the Heuningnes lineage. This study used an integrative approach to assess the taxonomic status of these three lineages. Detailed morphological examination identified a combination of characters that consistently separate the lineages, supporting their recognition as distinct species. Based on both genetic and morphological distinctiveness, we redescribe *P. burchelli* s.s. for the *P. burchelli* 'Tradouw' lineage, revalidate *Pseudobarbus vulneratus* (Castelnau, 1861) for the *P. burchelli* 'Breede' lineage, and describe the *P. burchelli* 'Heuningnes' lineage as a new species, *Pseudobarbus agulhas* **sp. nov.** These three species differ in circumpeduncular scale count, head and snout proportions, and the number of teeth in the outer pharyngeal tooth row. The biogeographic history, key threats, and conservation needs of these three species are discussed.

Key Words

Agulhas Plain, Breede, Cape Fold Ecoregion, Duiwenhoks, Goukou, Heuningnes, *Pseudobarbus agulhas* sp. nov., taxonomic revision, redfin minnows, Tradouw

Introduction

A combination of extensive biodiversity exploration and the application of integrated taxonomic approaches over the past two decades has resulted in an increase in the number of redfin species (genus *Pseudobarbus* Smith, 1841, Smiliogastrini) in southern Africa—from seven species in 2001 to 14 currently recognised species—due to the revalidation of synonyms and the description of new species (Skelton 2001, 2024; Chakona and Swartz 2013; Chakona et al. 2014; Chakona and Skelton 2017; Zarei et al. 2025a, b). Species of the genus *Pseudobarbus* are endemic to the Cape Fold Ecoregion (CFE) of South Africa (12 species), the southern temperate freshwater ecoregion of South Africa (one species), and the Highlands of Lesotho (one species) (Skelton 2024; Zarei et al. 2025a, b). Redfins are divided into two groups: the single-barbeled group (nine species) and the double-barbeled group (five species) (Skelton 2024; Zarei et al. 2025a, b). The monophyly of these groups is supported by molecular data (Yang et al. 2015). Interestingly, these two groups are allopatrically distributed, with the double-barbeled redfins confined to the southwestern and western parts of the CFE, ranging from the Verlorenvlei

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River system in the west to the Duiwenhoks River system in the south. In contrast, the single-barbeled redfins are mostly distributed in the southern river systems of the CFE, from the Gourits to the Sundays River system. Exceptions to this pattern include *Pseudobarbus phlegethon* (Barnard, 1938), which occurs in the Olifants-Doring system on the west coast; *Pseudobarbus kubhekai* Zarei, Mathebula & Chakona, 2025, found in the Mzimkhulu River system in the Southern Temperate Ecoregion; and *Pseudobarbus quathlambae* (Barnard, 1938), which occurs in streams of the upper Orange River system in the Lesotho Highlands (Skelton 2024; Zarei et al. 2025a, b). In *Pseudobarbus* spp., sexually active mature males typically develop conical or blunt tubercles on the snout and head.

Over the past two decades, dedicated exploration of river systems that encompass the distribution range of the double-barbeled redfins—including the Verlorenvlei, Berg, Breede, Heuningnes, Goukou, and Duiwenhoks river systems—and the use of molecular data have uncovered undocumented diversity within this group (Bloomer and Impson 2000; Chakona et al. 2013, 2014; Swartz et al. 2014). This led to the description of a new species, *Pseudobarbus verloreni* Chakona, Swartz & Skelton, 2014, endemic to the Verlorenvlei River system (Chakona et al. 2014). This species was previously included under *Pseudobarbus burgi*, which is now recognised as a valid species endemic to the Berg River (Bloomer and Impson 2000; Chakona et al. 2014). Four genetically distinct and allopatrically distributed lineages—*Pseudobarbus burchelli* 'Giant', *P. burchelli* 'Tradouw', *P. burchelli* 'Breede', and *P. burchelli* 'Heuningnes'—were identified within *P. burchelli*'s (Smith, 1841) distribution range (Swartz et al. 2009, 2014; Chakona et al. 2013). The Giant Redfin, *P. burchelli* 'Giant', was subsequently described as a new species, *Pseudobarbus skeltoni* Chakona & Swartz, 2013 (Chakona and Swartz 2013). Recently, in his revised book *Freshwater Fishes of Southern Africa*, Skelton (2024) revalidated *Pseudobarbus vulnerata* (Castelnau, 1861)—hereafter *Pseudobarbus vulneratus*; see the species' etymology below—for the Breede lineage, *P. burchelli* 'Breede'. The distribution range of *P. vulneratus* extends across three river systems: the Breede, Goukou, and Duiwenhoks (Swartz et al. 2009, 2014; Chakona et al. 2013; Skelton 2024). Following the principles of zoological nomenclature, Skelton (2024) designated the Tradouw lineage, *P. burchelli* 'Tradouw', as *P. burchelli* s.s. This followed an earlier decision where a specimen from the Tradouw River was designated as the neotype for this species (Skelton 1988). *Pseudobarbus burchelli* s.s. is thus confined to the Tradouw River sub-catchment in the Breede River system. The taxonomic status of the fourth lineage within the *P. burchelli* complex, i.e., *P. burchelli* 'Heuningnes', remains uncertain.

The purpose of the present study was to undertake a detailed morphological examination of specimens of *Pseudobarbus vulneratus* and *P. burchelli* s.s. in order to provide updated redescriptions of these species, as the original descriptions were not comprehensive. This is particularly important given the subtle morphological differences among the double-barbeled redfins from the CFE. Identification and documentation of diagnostic characters for these species is essential to support accurate species identification by officials involved in designing conservation plans for these highly threatened fishes. A second objective was to determine the taxonomic status of the *P. burchelli* 'Heuningnes' lineage and identify diagnostic characters separating this candidate species from the other two species in the *P. burchelli* complex. Therefore, we present both molecular and morphological evidence supporting the recognition of these three lineages within the *P. burchelli* complex as separate species and discuss immediate and long-term conservation measures needed to ensure their persistence.

Materials and methods

The study utilised fresh and museum specimens and tissue samples obtained from the National Fish Collection and the National Aquatics BioBank at the NRF–South African Institute for Aquatic Biodiversity (NRF–SAIAB). These specimens were collected following standardised sampling and field processing protocols approved by the NRF–SAIAB Animal Ethics Committee. The specimens were primarily collected using seine nets, hand nets or fyke nets. A subsample of the captured fish was selected for deposition into the National Fish Collection for future reference. Topotypes of *P. vulneratus* were collected from the type locality of this species, the Baviaans River near the town of Genadendal in the Riviersonderend sub-catchment of the Breede River system (Castelnau 1861). Additional comparative material from populations in the Breede, Goukou, and Duiwenhoks river systems was included to document intraspecific morphological variation within this species. Topotypes of *P. burchelli* s.s. were collected from the Huis and Tradouw rivers. Samples representing the *P. burchelli* 'Heuningnes' lineage were collected from the Heuningnes River system, as well as from the recently identified population in the Klein River system in the Agulhas Plain. Specimens were anaesthetised with clove oil and photographed in the field to capture live colouration patterns. Tissue samples were collected for DNA analysis, preserved in 96% ethanol, and stored at –80 °C in the NRF-SAIAB BioBank. Source specimens were fixed in 10% formalin in the field and later transferred to 70% ethanol for long-term storage.

Genomic DNA was extracted using the salting-out method described by Bruford et al. (1992). Polymerase chain reaction (PCR) amplification and Sanger sequencing were performed on the mitochondrial *Cyt b* marker using the primer pair GluF/ThrR (Machordom and Doadrio 2001). Sequence chromatograms were visualised and edited using BioEdit 7.0.4 (Hall 1999). The newly generated sequences were deposited in GenBank [Molecular IDs:

SB11134–SB11138 (GenBank: PV699562–PV699566) and SB11145–SB11146 (GenBank: PV699567–PV699568) for the *P. burchelli* 'Heuningnes' lineage and SB13381–SB13384 (GenBank: PV699558–PV699561) for the *P. burchelli* 'Tradouw' lineage]. Additionally, the molecular dataset included 180 archived *Cyt b* sequences of double-barbeled *Pseudobarbus* species from previous studies (Tsigenopoulos et al. 2002; Chakona et al. 2013, 2014; Swartz et al. 2014) (Table 1).

Sequence alignment was conducted using ClustalW in MEGA 11 (Tamura et al. 2021). The optimal nucleotide substitution model was identified using the Akaike Information Criterion (AIC) in jModelTest 2.1.3 (Darriba et al. 2012). To assess nucleotide substitution saturation, we applied the test by Xia et al. (2003) using DAMBE 7 (Xia 2018). Phylogenetic reconstruction was performed using maximum likelihood (ML) analysis in RAxML 7.2.5 (Stamatakis 2006), incorporating a sequence of the single-barbeled species, *Pseudobarbus tenuis* (Barnard, 1938), as the outgroup. A median-joining (MJ) haplotype network was constructed in PopART 1.7 (Leigh and Bryant 2015). Average sequence divergence among double-barbeled *Pseudobarbus* species and lineages was estimated using the Kimura-2-Parameter (K2P) model in MEGA. Molecular species delimitation was conducted using three approaches: a distance-based method, Assemble Species by Automatic Partitioning (ASAP; Puillandre et al. 2021); a network-based method, reversed Statistical Parsimony (SP; Hart and Sunday 2007); and a tree-based method, Bayesian Poisson Tree Process (bPTP; Zhang et al. 2013).

Morphometric and meristic measurements followed the criteria established by Chakona and Skelton (2017), with additional morphometric characters included to document variation in head and body morphology. Specimens were measured using a digital calliper. Standard length (SL) is defined as the distance from the median anterior point of the upper lip to the posterior end of the hypurals. Following Randall (2001), morphometric data are presented as ratios in the text and as percentages of SL and head length (HL) in the accompanying table. Osteological terminology follows Skelton (1988). Osteological examination was based on X-ray images captured with an Inspex 20i Digital X-ray Imaging System (Kodex Inc., New Jersey, USA) at NRF-SAIAB. Statistical analyses were performed using IBM SPSS Statistics 27. The entire branchial basket, including the pharyngeal bones, was dissected from five specimens per species to count the gill rakers on the first arch and the pharyngeal teeth (the terminology of pharyngeal tooth rows follows Skelton (1988)). Pharyngeal tooth formulae follow the format x–y,x–y,x–y + x–y,x–y,x–y, indicating the number of teeth in the outer, middle, and inner rows of the left arch and the inner, middle, and outer rows of the right arch, respectively; '+' separates the left and right arches, and '–' denotes variation in tooth counts. Gill rakers on the first arch are presented as x–y+x–y+x–y, representing epibranchial, angle, and ceratobranchial rakers, respectively; '+' separates regions and '–' denotes observed count ranges.

The terminology for head tubercles follows Skelton (1988). A consistent pattern of tubercle distribution on the snout and head is observed within the genus *Pseudobarbus*: (i) bilateral clusters of tubercles develop on the snout; (ii) a row of progressively smaller tubercles extends in an arc above each nare to the antero-dorsal edge of the orbit; (iii) this row continues posteriorly along the dorsal edge of each orbit; and (iv) smaller tubercles are scattered irregularly across the crown of the head, typically forming an anterior and a posterior cluster, referred to as the anterior dorsal and posterior dorsal clusters, respectively.

Institutional abbreviations: NRF-SAIAB: National Research Foundation-South African Institute for Aquatic Biodiversity, Makhanda, South Africa. BMNH: Natural History Museum, London, UK. USNM: Smithsonian Institution National Museum of Natural History, Department of Vertebrate Zoology, Division of Fishes, Washington DC, USA. MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

Table 1. List of 191 double-barbeled *Pseudobarbus* specimens (55 haplotypes) used in the molecular analyses (Cyt b), including GenBank accession numbers. The geographic distribution of the specimens is shown in Fig. 2.

Species/lineage	N	Sequence ID	Locality	Reference
P. burchelli 'Tradouw'	4	SB13381–SB13384 (GenBank: PV699558–PV699561)	Tradouw catchment, Breede River system	This study
	20	EU341738–EU341754, KF222700–KF222702	Tradouw catchment, Breede River system	Swartz et al. (2014); Chakona et al. (2013)
P. burchelli 'Breede'	125	EU341714–EU341729, KF222668–KF222699, KF222708–KF222741, KF222746–KF222759, KF222761–KF222786, KF222789–KF222791	Breede, Duiwenhoks, and Goukou river systems	Swartz et al. (2014); Chakona et al. (2013)
P. burchelli 'Heuningnes'	20	EU341730–EU341737, KF222703–KF222707, KF222742–KF222745, KF222760, KF222787–KF222788	Heuningnes River system	Swartz et al. (2014); Chakona et al. (2013)
P. burchelli 'Heuningnes'	7	SB11134–SB11138 (GenBank: PV699562–PV699566), SB11145–SB11146 (GenBank: PV699567–PV699568)	Klein River system	This study
P. burgi	1	AF180849	Berg River system	Tsigenopoulos et al. (2002)
P. verloreni	2	KM366106–KM366107	Verlorenvlei River system	Chakona et al. (2014)
P. skeltoni	12	KF222577–KF222588	Riviersonderend River, Breede River system	Chakona et al. (2013)

N, number of sequences.

Results

Molecular data

JModelTest identified GTR+G as the optimal substitution model for the 676 bp *Cyt b* dataset, which included 191 individuals representing all double-barbeled *Pseudobarbus* species and lineages, as well as one outgroup, *P. tenuis* (Barnard, 1938). Analysis of nucleotide substitution patterns indicated that the sequences had not reached saturation (Iss < Iss.c S / Iss.c A), confirming their suitability for phylogenetic analysis. The Maximum Likelihood (ML) phylogenetic tree incorporated new sequences from 11 *Pseudobarbus* individuals (SB11134–SB11138 and SB11145–SB11146 for the *P. burchelli* 'Heuningnes' lineage, and SB13381–SB13384 for the *P. burchelli* 'Tradouw' lineage), as well as 49 archived haplotypes from GenBank (Fig. 1).

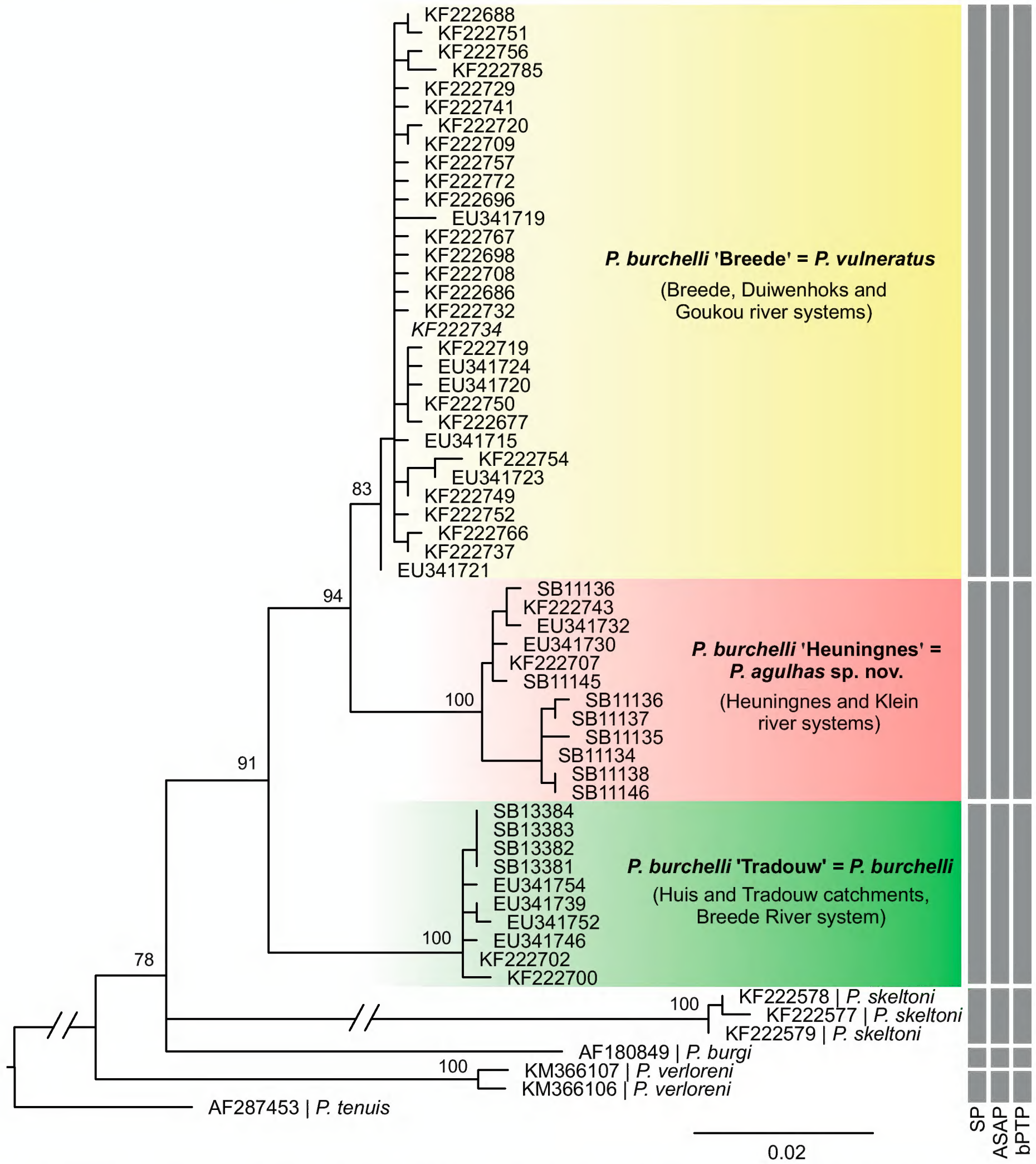

Figure 1. Maximum likelihood (ML) phylogeny of double-barbeled *Pseudobarbus* species and lineages based on 55 Cyt b haplotypes (191 sequences). *Pseudobarbus tenuis*, a single-barbeled species, represents the outgroup. The grey bars on the right indicate the results of species delimitation analyses.

Consistent with previous findings, samples originally identified through morphological examination or referenced literature as *P. burchelli* were recovered in three major clades (Fig. 1). A clade corresponding to the *P. burchelli* 'Tradouw' lineage, as defined by Swartz et al. (2009), includes samples from the Huis and Tradouw rivers, tributaries of the Breede River system (Fig. 2). The Tradouw River is the type locality of the neotype of *P. burchelli* (Skelton 1988). A second clade corresponds to the *P. burchelli* 'Breede' lineage (Swartz et al. 2009), distributed in the Breede, Goukou, and Duiwenhoks river systems (Fig. 2). This lineage includes the topotypes of *Pseudobarbus vulneratus* (originally described as *Gnathendalia vulnerata* Castelnau, 1861), based on specimens collected from the Baviaans River near the town of Genadendal, a tributary of the Riviersonderend River in the Breede River system. A third clade, identified as the *P. burchelli* 'Heuningnes' lineage (Swartz et al. 2009), is currently known from the Heuningnes River system and a recently discovered population in the upper catchment of the Klein River system (Fig. 2). The double-barbeled redfins are separated by considerable genetic differences (2.6–9.0%; Table 2). *Pseudobarbus burchelli* 'Breede' and *P. burchelli* 'Heuningnes' are sister lineages, separated by 2.6% K2P genetic distance (11 mutational steps; Fig. 3), forming a clade that is sister to *P. burchelli* 'Tradouw'. *Pseudobarbus burchelli* 'Tradouw' is separated from *P. burchelli* 'Breede' and *P. burchelli* 'Heuningnes' by 3.5% (19 mutations) and 4.5% (24 mutations) genetic distance, respectively (Table 2, Figs 1, 3). The three independent molecular species delimitation methods (SP, bPTP, and ASAP) consistently identified six putative species within the *Cyt b* dataset, which includes haplotypes representing four nominal species (Fig. 1). All delimitation approaches supported the recognition of the *P. burchelli* 'Tradouw', *P. burchelli* 'Breede', and *P. burchelli* 'Heuningnes' lineages as distinct taxonomic entities.

Table 2. Average K2P genetic distance (%) between double-barbeled *Pseudobarbus* species and lineages based on 191 Cyt b sequences (55 haplotypes).

		1	2	3	4	5	6
1	*P. burchelli* 'Breede'						
2	*P. burchelli* 'Heuningnes'	2.6					
3	*P. burchelli* 'Tradouw'	3.5	4.5				
4	*P. verloreni*	6.4	7.2	6.7			
5	*P. skeltoni*	8.4	8.4	7.9	9.2		
6	*P. burgi*	6	5.9	6.9	7.3	9	

Morphological descriptions

Detailed morphological examination also revealed that the three *P. burchelli* lineages differ in scale counts, head and snout proportions, and the number of teeth in the outer pharyngeal tooth row (see taxonomic accounts). Based on the combination of molecular and morphological differences, as well as geographical separation, we herein redescribe *P. burchelli* s.s. (i.e., the *P. burchelli* 'Tradouw' lineage) and *P. vulneratus* (i.e., the *P. burchelli* 'Breede' lineage) and describe a new species, *Pseudobarbus agulhas* sp. nov., for the *P. burchelli* 'Heuningnes' lineage.

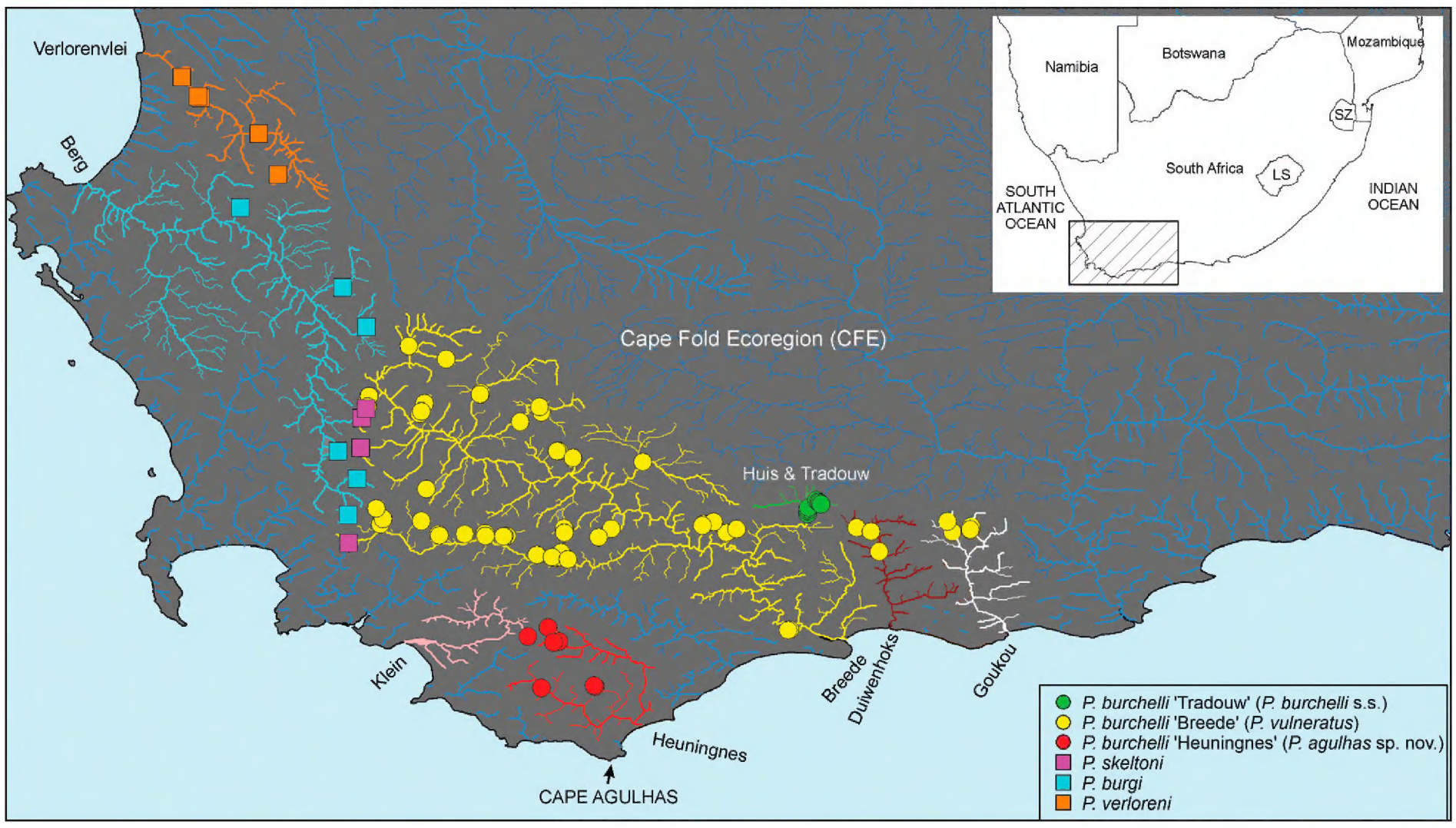

Figure 2. Distribution map of all double-barbeled *Pseudobarbus* species/lineages based on genetic data (this study; Bloomer and Impson 2000; Tsigenopoulos et al. 2002; Chakona et al. 2013, 2014; Swartz et al. 2014).

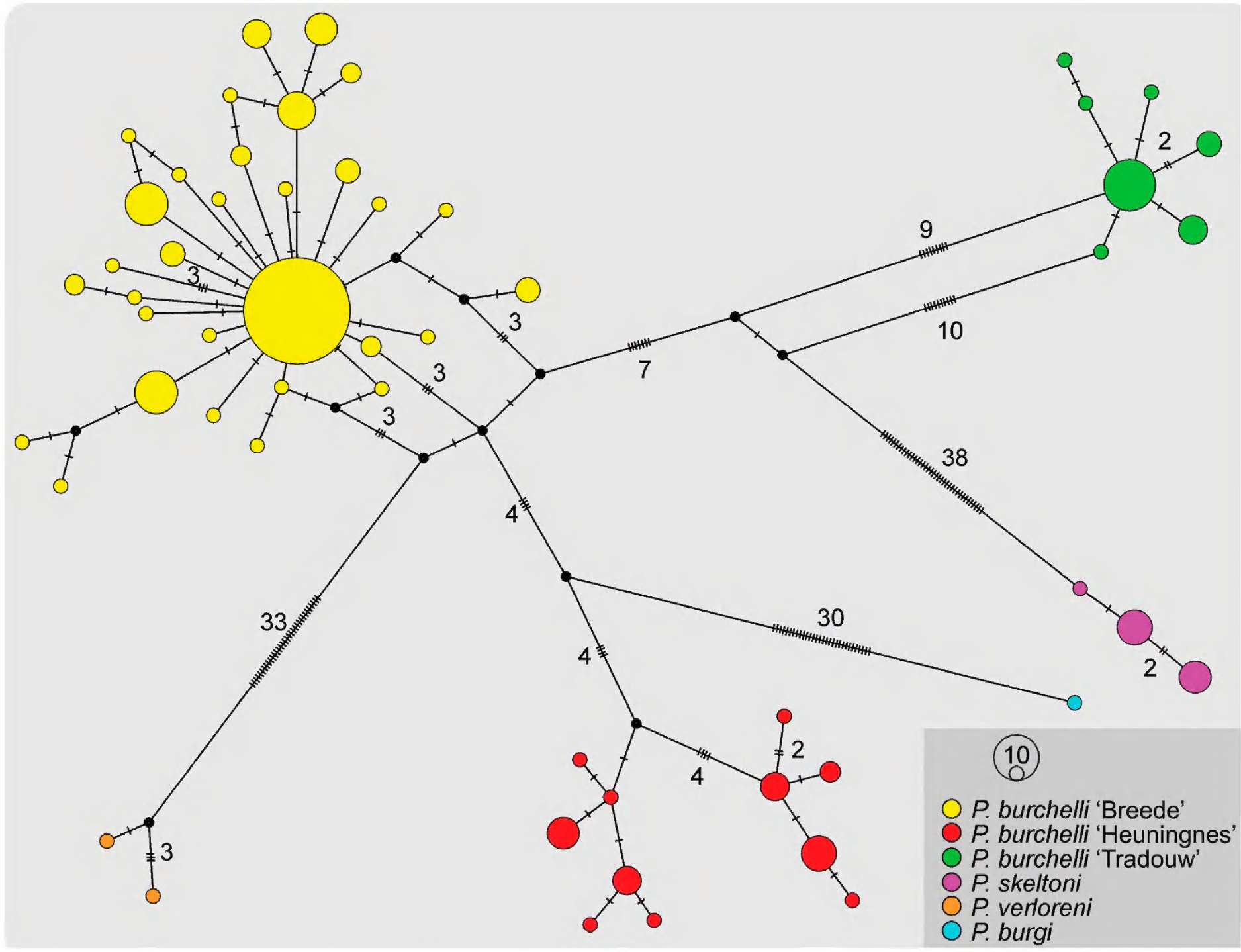

Figure 3. Median-joining (MJ) haplotype network for 191 Cyt b sequences (55 haplotypes) of double-barbeled *Pseudobarbus* species and lineages. Mutational steps between adjacent haplotypes are denoted by hatch marks and numbers. Circle sizes reflect the relative abundance of each haplotype, with colours representing different species and lineages. Hypothetical haplotypes are indicated by small black circles.

Taxonomic accounts

Pseudobarbus burchelli (Smith, 1841)

English name: Tradouw redfin / Barrydale redfin

Afrikaans name: Tradouw-rooivlekie / Barrydale-rooivlekie

Figs 4, 5

Barbus (*Pseudobarbus*) *burchelli* Smith, 1841: no pagination, pl XI, no. 1 (Tradouw River, Breede River system, southwestern Cape Province, South Africa, -33.947222, 20.710833).

Pseudobarbus burchelli – Skelton 1988:264; Skelton 2024:245.

Neotype. • SAIAB 126387 (AMG/P 7223), 102 mm SL, Tradouw River, Breede River system, South Africa, -33.9472, 20.71083, collected by S. Thorne, 13 December 1978. Neotype designated by Skelton (1988).

Additional material (n = 28). • SAIAB 200882 (tag numbers X2–X10), 9 specimens, 68.6–91.7 mm SL, Tradouw River, Breede River system, South Africa, -33.9358, 20.7094, collected by A. Chakona & E. Swartz, 16 February 2009. • SAIAB 200876 (tag numbers M1–M6), 6 specimens, 63.9–98.4 mm SL, Tradouw River, Breede River system, South Africa, -33.9567, 20.7078, collected by A. Chakona & E. Swartz, 15 February 2009. • SAIAB 200877 (tag numbers M7–M10), 4 specimens, 56.8–83.9 mm SL, Tradouw River, Breede River system, South Africa, -33.91575, 20.7464, collected by A. Chakona & E. Swartz, 15 February 2009. • SAIAB 200880, 4 specimens, 72.5–84.6 mm SL, Moeras, Tradouw River, Breede River system, South Africa, -33.9212, 20.752972, collected by A. Chakona & E. Swartz, 15 February 2009; • SAIAB 235751, 5 specimens, 78.2–106.8 mm SL, Huis River, Breede River system, South Africa, -33.92225, 20.75361, collected by A. Chakona, P. Bragança, P.H. Skelton & M. Jordaan, 12 April 2022.

Diagnosis. *Pseudobarbus burchelli* is diagnosed among all currently recognised congeners by the following combination of character states: mouth subterminal, with two pairs of barbels; head length 25.7–28.8% SL; interorbital width 32.7–37.5% HL; anterior barbel length 9.4–26.4% HL; orbit diameter 18.5–24.2% HL; head width (at operculum 62.4–71.5% HL, at eye 49.3–53.9% HL, at mouth corner 37.4–43.6% HL); lateral-line scale count 35–38, usually 35–37; circumpeduncular scale count 14–16, usually 15–16; absence of linear stripes; presence of dorsal spots and mid-lateral blotches

Figure 4. *Pseudobarbus burchelli*, SAIAB 126387, male, neotype, 102 mm SL, Tradouw, Breede River system. **A.** lateral view; **B.** dorsal view.

on the body; tuberculation of head in mature breeding males: large to small conical/blunt tubercles, 3–10 in each snout cluster, single row above each naris with 2–5 tubercles per cluster, and single row above each orbit with 2–6 tubercles per cluster; and 2–3, usually 2 teeth in the outer pharyngeal tooth row. Additionally, *Pseudobarbus burchelli* is the only redfin species found in the Huis and Tradouw catchments of the Breede River system.

Description. All morphometric values in the text are presented as neotype first and additional material, if different, in parentheses.

***General morphology*.** Body proportions and meristic data are provided in Table 3. Body moderately elongated, fusiform; dorsal profile more convex than ventral; max body depth in front of dorsal fin 3.5 (3.6–4.4) in SL; laterally compressed. Caudal peduncle shallow, depth 0.5 (0.5–0.6) times caudal-peduncle length. Head large, length 3.5 (3.5–3.9) in SL, depressed, depth at eye 6.4 (6.1–7.1) in SL and 0.5 (0.5–0.7) times maximum body depth. Postorbital profile steep. Snout blunt, short, oblique, convex; longer than eye, length 2.0 (1.4–1.9) times eye diameter and 2.7 (2.7–3.1) in head length. Eyes large; diameter 5.4 (4.1–5.1) in head length; dorsolateral, not above dorsal profile, closer to tip of snout than posterior margin of operculum. Interorbital broad and flat, 1.9 (1.4–1.8) times eye diameter. Mouth sub-terminal, sickle-shaped; corner reaches vertical line through middle of nares. Mouth has two pairs of prominent barbels. Anterior barbel length variable, length 1.3 (0.5–1.2) times orbit diameter, ranging from significantly short of anterior eye margin to extending to the mid-point of the eye. Posterior barbel length variable, 2.5 (0.7–2.2) times orbit diameter, ends between mid-point of eye and slightly beyond preopercular margin.

Figure 5. Live specimens of *Pseudobarbus burchelli* (SAIAB 235751) from the Huis River, Breede River system.

Tuberculation. Mature breeding males display conical tubercles (neotype) or typically blunt tubercles of varying sizes on the snout and top of the head. Bilateral clusters of large tubercles, ranging from 3 to 10 per cluster, present on the snout (Fig. 6). An arc of tubercles, varying from large to small and resembling snout tubercles, extends above each naris (2–5 per cluster) to the antero-dorsal edge of the orbit. This continues posteriorly with a single row of 2–6 tubercles along the dorsal edge of each orbit, larger in the front. The anterior dorsal cluster features several small or tiny tubercles, while the posterior dorsal cluster contains scattered minute tubercles that gradually decrease in size towards the back. In the neotype, a row of minute tubercles is found along the free edge of all body scales, with the exception of the ventral scales located anterior to the pelvic origin. The dorsal and pectoral fin rays of the neotype display 1–2 lines of minute tubercles. In contrast, the other examined specimens showed no tubercles on the fin rays or the free edges of their body scales.

Scales. LL 35–38 (neotype: 37; other material: 35:4, 36:9, 37:5, 38:1), LD 5–7 (neotype: 6; other material: 5:1, 6:16, 7:2), LP 4–5 (neotype: 5; other material: 4:1, 5:18), LA 4–5 (neotype: 5; other material: 4:4, 5:15), CP 14–16 (neotype: 14; other material: 14:2, 15:5, 16:10), PDS 14–18 (neotype: 15; other material: 14:1, 15:6, 16:5, 17:5, 18:2). The predorsal scales, located between the back edge of the head and the start of the dorsal fin, are smaller and embedded compared to the scales on the flanks. The ventral scales between the origins of the pectoral and pelvic fins are reduced and embedded. All scales cycloid.

Fins. Dorsal fin rays iv/7; anal fin rays iv/5–iv/6 (neotype: iv/5; other material: iv/5:17, iv/6:2); pectoral fin rays 13–16 (neotype: 14; other materials: 13:5, 14:9, 15:4, 16:1); pelvic fin rays 8; caudal fin branched rays 17. The dorsal fin is positioned nearly in the centre of the body (not counting the caudal fin), with its origin just behind the vertical line that runs through the pelvic fin's origin; the distal edge is straight or slightly concave, and the tip of the lowered dorsal fin is 1–3 scales short of the vertical line at the rear base of the anal fin. The pectoral fin exhibits a fan-like morphology and shows variability in length, either reaching or exceeding the origin of the pelvic fins in both sexes

Table 3. Morphometric and meristic data for *Pseudobarbus burchelli*, *P. vulneratus* and *P. agulhas* sp. nov.

		P. burchelli		*P. vulneratus*		*P. agulhas* sp. nov.	
Character	**Acronym**	**Neotype**	**Neotype + other materials (N = 20)**	**Neotype**	**Neotype + other materials (N = 56)**	**Holotype**	**Holotype + paratypes and additional materials (N = 35)**
Standard length	SL	98.6	55.8–98.6	67.3	40.1–89.4	69.9	45.6–88.1
% of SL							
Head length	HL	28.2	25.7–28.8	27.2	24.2–29.8	27.5	25.6–31.4
Pre-dorsal length	PDL	52.8	51.9–55.6	53.3	49.1–57.6	53.2	50.3–54.5
Body depth at pelvic origin*	BDp	28.7	21.7–28.7	24.0	20.0–28.1	25.0	21.2–27.9
Max body depth anterior to dorsal fin*	BDm	29.0	22.6–29.0	23.8	20.1–27.6	25.1	22.1–27.9
Dorsal fin base	DB	14.0	12.2–14.0	12.7	10.9–15.5	13.2	11.8–15.1
Dorsal fin height	DH	20.9	18.9–23.6	23.7	17.8–24.9	22.4	20.3–26.2
Pectoral fin length	PtL	19.6	16.3–22.5	23.8	17.4–24.4	20.0	19.2–24.3
Pelvic fin length	PvL	16.5	13.6–17.5	17.0	13.8–18.9	16.3	15.5–18.6
Anal fin base	AfB	11.8	10.1–11.8	11.9	8.9–14.2	10.6	9.0–12.0
Anal fin height	AfH	18.4	17.3–21.3	20.8	16.4–22.5	19.8	19.2–22.1
Caudal peduncle length	CPL	25.8	22.4–26.0	24.7	22.1–27.9	22.3	21.0–27.0
Caudal peduncle depth	CPD	13.8	11.2–13.8	12.4	9.4–14.6	11.6	10.0–13.4
Min width of caudal peduncle*	CPW	5.4	4.3–5.8	5.5	3.1–7.0	4.3	4.3–7.0
Pectoral to pelvic fin length	PP	22.9	21.4–26.0	21.8	19.5–27.8	26.5	21.1–26.5
Pelvic to anal fin length	PA	13.5	13.5–16.6	13.0	12.3–20.7	15.2	12.4–19.8
Preanal-fin distance*	PAD	66.0	66.0–71.0	65.0	63.7–72.1	70.3	64.9–71.3
Body width	BW	21.3	13.5–21.3	17.7	12.7–24.3	17.3	13.4–18.7
% of HL							
Max head width at operculum*	HW	71.5	62.4–71.5	65.8	54.4–69.0	56.4	53.1–61.6
Head width at eye*	HWE	53.2	49.3–53.9	50.0	40.5–55.0	48.5	43.1–48.9
Snout length	S	36.5	31.8–37.7	38.6	26.0–39.8	35.4	30.7–37.6
Snout depth at nares*	SD	38.1	33.0–43.4	36.5	29.4–41.7	38.5	32.9–41.0
Snout (head) width at mouth corner*	SW	37.4	37.4–43.6	39.7	28.1–42.0	32.9	29.7–37.3
Left to right naris*	ND	18.8	18.8–22.7	20.4	16.9–25.5	19.5	16.8–21.6
Orbit diameter	OD	18.5	18.5–24.2	22.1	18.1–27.2	21.3	18.4–26.4
Inter-orbit length	IO	34.7	32.7–37.5	35.9	28.1–39.8	37.4	32.3–38.7
Post-orbit length	PO	47.4	46.0–50.7	45.6	38.4–50.1	47.1	42.8–49.2
Head depth at posterior edge of nape*	HDn	69.3	64.5–70.3	70.8	61.7–75.9	67.1	62.3–73.2
Head depth at eye*	HDe	55.2	52.1–57.7	56.2	45.4–59.0	54.4	48.6–66.5
Head depth at preopercular margin*	HDp	66.0	61.9–68.1	67.0	56.5–70.9	64.1	59.8–68.5
Cheek depth*	CD	28.5	24.4–29.5	27.4	20.1–30.4	24.9	21.8–28.7
Anterior barbel length	AB	24.6	9.4–26.4	20.4	6.8–31.2	17.7	8.4–24.8
Posterior barbel length	PB	45.4	14.7–45.4	30.2	7.4–47.6	31.0	22.0–42.1
Meristics							
Lateral line scales (total)	LL	37	35–38	36	32–39	37	34–39
Lateral line to dorsal fin scales	LD	6	5–7	6	5–7	7	6–8
Lateral line to pelvic fin scales	LP	5	4–5	4	4–6	4	4–6
Lateral line to anal fin scales	LA	5	4–5	5	4–6	4	4–6
Caudal peduncle scales	CP	14	14–16	12	12–13	15	14–16
Predorsal scales	PDS	15	14–18	17	14–18	15	15–18
Dorsal fin rays (unbranched/branched)	BdR	iv/7	iv/7	iv/7	iv/6– iv/8	iv/7	iv/7– iv/8
Anal fin rays (unbranched/branched)	BaR	iv/5	iv/5–iv/6	iv/5	iv/5	iv/5	iv/5–iv/6
Pectoral fin rays	PecR	14	13–16	14	13–15	14	14–16
Pelvic fin rays	PelR	8	8–8	8	7–8	8	8–9
Total vertebrae	TV	36	36–36	36	34–38	37	36–37
Pre-dorsal vertebrae	PdV	12	11–12	12	11–13	11	11–12
Pre-caudal vertebrae	PcV	20	19–20	20	19–21	19	19–21
Caudal vertebrae	CV	16	16–17	16	15–18	18	16–18

* Additional morphometric characters (not examined by Chakona and Skelton 2017) included to document head and body morphometric variation.

or being 1–4 scales shorter. The origin of the pelvic fin is positioned slightly anterior to the origin of the dorsal fin; their length is variable, with the tip of the lowered pelvic fin either reaching or falling 1–3 scales short of the anterior origin of the anal fin in both sexes. The distal margin of the anal fin is nearly straight to slightly convex, with its origin located closer to the anterior base of the pelvic fin than to the base of the caudal fin. The caudal fin is forked.

Osteology (n = 5). Vertebral column including Weberian apparatus and urostyle: total vertebrae 36, predorsal vertebrae 11–12 (neotype: 12; other material: 11:1, 12:3), precaudal vertebrae 19–20 (neotype: 20; other material: 19:2, 20:2), caudal vertebrae 16–17 (neotype: 16; other material: 16:2, 17:2).

Gill rakers (n = 5). 2–4+1+7–12 (epibranchial: 2:1, 4:4; angle: 1:5; ceratobranchial: 7:1, 11:3, 12:1).

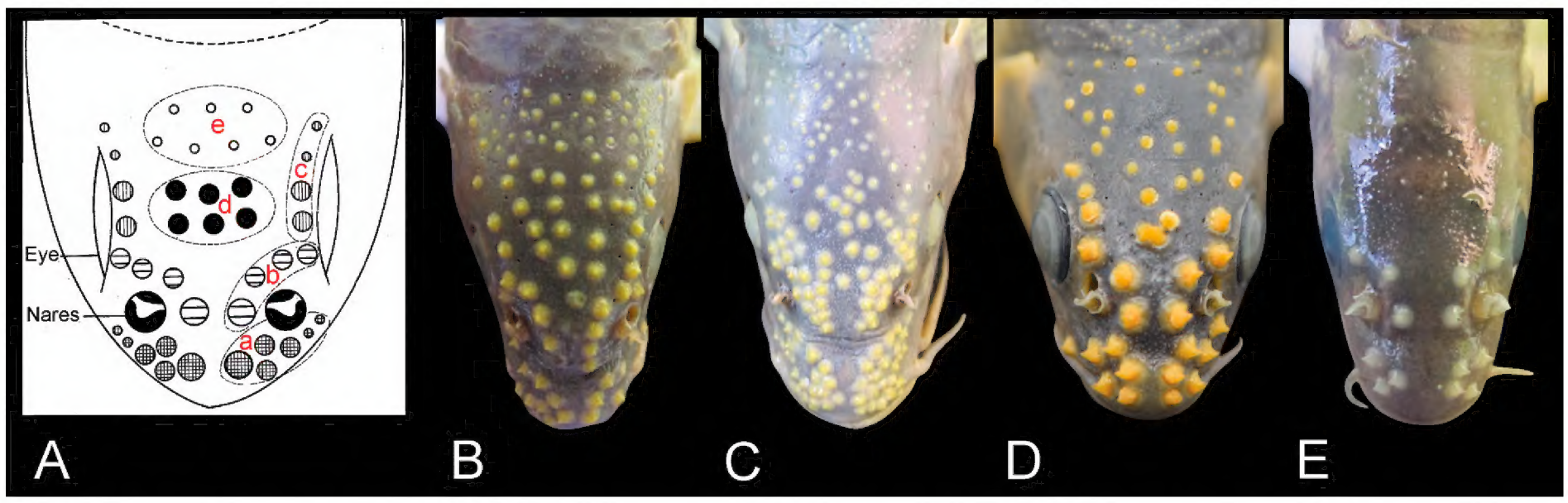

Figure 6. A. Diagrammatic representation of the head tubercle pattern in a mature breeding male redfin: a, cluster on snout; b, row above nares; c, row above orbit; d, anterior dorsal cluster; e, posterior dorsal cluster (modified from Skelton 1988). Tuberculation of head in mature breeding males of **B.** *Pseudobarbus burchelli* (SAIAB 126387, neotype, 102 mm SL, Tradouw catchment, Breede River system); **C.** *P. skeltoni* (SAIAB 187243, holotype, 158.2 mm SL, Riviersonderend River upstream, Breede River system); **D.** *P. vulneratus* (SAIAB 210457, 63.6 mm SL, Duiwenhoks River system), and **E.** *P. agulhas* sp. nov. (SAIAB 246288, 66.4 mm SL, Klein River system).

Pharyngeal teeth (n = 5). Three rows of pharyngeal teeth, teeth pattern 2–3,2–3,4–5 + 4–5,2–3,2. The distribution frequency of pharyngeal teeth is given in Table 4.

Colour of live specimens. Refer to Fig. 5 for live colouration. Dorsal colour dark golden-brown to olive-brown; ventral colour white to yellowish white. Fins with bright scarlet bases, less intense in caudal fin. Mid-lateral band distinct or indistinct; if distinct, typically with large triangular mark at caudal base. Dorsum features dark brown spots and blotches; irregular spots may also occur along posterior body.

Colour of preserved specimens (Fig. 4). The flanks typically display a distinct dark brown mid-lateral band that terminates in a triangular shape just anterior to the base of the caudal fin; this band may be less pronounced or absent in darker individuals and breeding males. The dorsal head and body are dark or dark brown, transitioning to a lighter colour ventrally. Dorsal spots and mid-lateral blotches were absent in the examined specimens.

Distribution and ecology. *Pseudobarbus burchelli* has a limited distribution, being confined to the Huis and Tradouw rivers within the Breede River system (Fig. 2; Swartz et al. 2009, 2014; Chakona et al. 2013, 2024).

It has been recorded to occur in deep rocky pools and flowing rocky runs (Skelton 2024).

Conservation. This lineage is classified as Critically Endangered (CR) in the latest IUCN Red List Assessment for freshwater fishes of South Africa (Chakona et al. 2022; Skelton 2024). Its restricted population is under threat from introduced smallmouth bass, water abstraction for urban and agricultural use, and deterioration of water quality (Skelton 2024).

Etymology. The species is named after William Burchell (1781–1863), a naturalist and early explorer of South Africa (Skelton 1988).

Comparison with other species

Pseudobarbus burchelli is readily identifiable from *P. afer* (Peters, 1864), *P. asper* (Boulenger, 1911), *P. kubhekai* Zarei, Mathebula & Chakona, 2025, *P. outeniqua* Zarei, Bragança, Skelton & Chakona, 2025, *P. phlegethon* (Barnard, 1938), *P. quathlambae* (Barnard, 1938), *P. senticeps* (Smith, 1936), *P. swartzi* Chakona & Skelton, 2017, and *P. tenuis*, by having two pairs of oral barbels (vs. a single pair). *Pseudobarbus burchelli* differs from *P. skeltoni* in maximum body length (98.6 vs. 163.4 mm SL, largest size of any *Pseudobarbus* species), head length (25.7–28.8 vs. 28.5–35.6% SL), interorbital width (32.7–37.5 vs. 23.9–32.3% HL), mouth morphology (subterminal in all size classes vs. terminal in adults), tuberculation of head in mature breeding males (large to small conical/blunt tubercles, 3–10 in each snout cluster, single row above each naris with 2–5 tubercles per cluster, and single row above each orbit with 2–6 tubercles per cluster vs. large prominent conical tubercles, 22–30 in each snout cluster, multiple rows above each naris with 6–16 tubercles per cluster, and multiple rows above each orbit, with up to 12 tubercles per cluster; Fig. 6), and distribution (Huis and Tradouw rivers in the Breede River system vs. upper Riviersonderend River, a major tributary

Table 4. Distribution frequency of pharyngeal teeth in the *Pseudobarbus burchelli* complex.

Species		Left pharyngeal							Right pharyngeal						
		Outer row			Middle row		Inner row		Inner row		Middle row		Outer row		
	N	1	2	3	2	3	4	5	4	5	2	3	0	1	2
P. burchelli	5		4	1	1	4	3	2	3	2	1	4			5
P. vulneratus	5		5			5	2	3	2	3	1	4			5
P. agulhas sp. nov.	5	3	2			5	4	1	5		2	3	1	4	

N, number of specimens.

of the Breede River, and the Krom River, a tributary of the Molenaars River in the Breede River system). *Pseudobarbus burchelli* differs from *P. burgi* in anterior barbel length (9.4–26.4 vs. 0.9–9.1% HL and only present in specimens above 40 mm SL), tuberculation of head in mature breeding males (large to small conical/blunt tubercles, 3–10 in each snout cluster vs. large conical tubercles, 10–15 in each snout cluster), absence of linear stripes on the body above and below the mid-lateral band (vs. present, Fig. 7), and distribution (Huis and Tradouw rivers in the Breede River system vs. the Great Berg River system and formerly in the Eerste River). *Pseudobarbus burchelli* differs from *P. verloreni* in anterior barbel length (9.4–26.4 vs 6.3% HL for the holotype and 3.3 ± 0.3% HL for the paratypes), orbit diameter (18.5–24.2 vs. 31.2% HL for the holotype and 31.5 ± 0.4% HL for the paratypes), lateral-line scale count (35–38, usually 35–37 vs. 29–36, usually 32), absence of linear stripes on the body above and below the mid-lateral band (vs. present, Fig. 7), tuberculation of head in mature breeding males (large to small conical/blunt tubercles, 3–10 in each snout cluster vs. tubercles confined to snout with 2 in each cluster), and distribution (Huis and Tradouw rivers in the Breede River system vs. the Verlorenvlei River system). *Pseudobarbus burchelli* differs from *P. vulneratus* in circumpeduncular scale count (14–16, usually 15–16 vs. 12–13) and distribution (Huis and Tradouw rivers in the Breede River system vs. Breede, Duiwenhoks and Goukou river systems). *Pseudobarbus burchelli* differs from *P. agulhas* sp. nov. in having a wider head (maximum head width 62.4–71.5% HL, head width at eye 49.3–53.9% HL, and snout width at mouth corner 37.4–43.6% HL vs. maximum head width 53.1–61.6% HL, head width at eye 43.1–48.9% HL, and snout width at mouth corner 32.4–37.3% HL), teeth count in the outer pharyngeal tooth row (2–3, usually 2 vs. 0–2, usually 1), and distribution (Huis and Tradouw rivers in the Breede River system vs. Heuningnes and Klein River systems).

Pseudobarbus vulneratus (Castelnau, 1861)

English name: Breede River redfin

Afrikaans name: Breederivier-rooivlerkie

Figs 8, 9

Gnathendalia vulnerata Castelnau, 1861:57 (Tributary of Breede River at Moravian mission of Genadendal, Cape Province, South Africa).

Barbus multimaculatus Steindachner, 1870:633, Pl. 3 (fig. 2).

Pseudobarbus burchelli Smith, 1841 – Skelton 1988:264, 1993:123, 2001:123 (in part).

Pseudobarbus vulnerata (Castelnau, 1861) – Skelton 2024:248; Zarei et al. 2025a:2.

Neotype designation for *Pseudobarbus vulneratus* (Castelnau, 1861). The original syntypes of *Pseudobarbus vulneratus* [BMNH (skins), not found], described by Castelnau (1861), are currently untraceable. To ensure taxonomic stability (in accordance with Art. 75.3 of the ICZN), we designate a neotype from the type locality—

Figure 7. Fresh and live specimens showing the presence of linear speckles on the body in **A.** *Pseudobarbus burgi* (SAIAB 200355, 68 mm SL, Tierkloof River, Berg River system) and **B.** *P. verloreni* (SAIAB 186092, holotype, 70.8 mm SL, Verlorenvlei River).

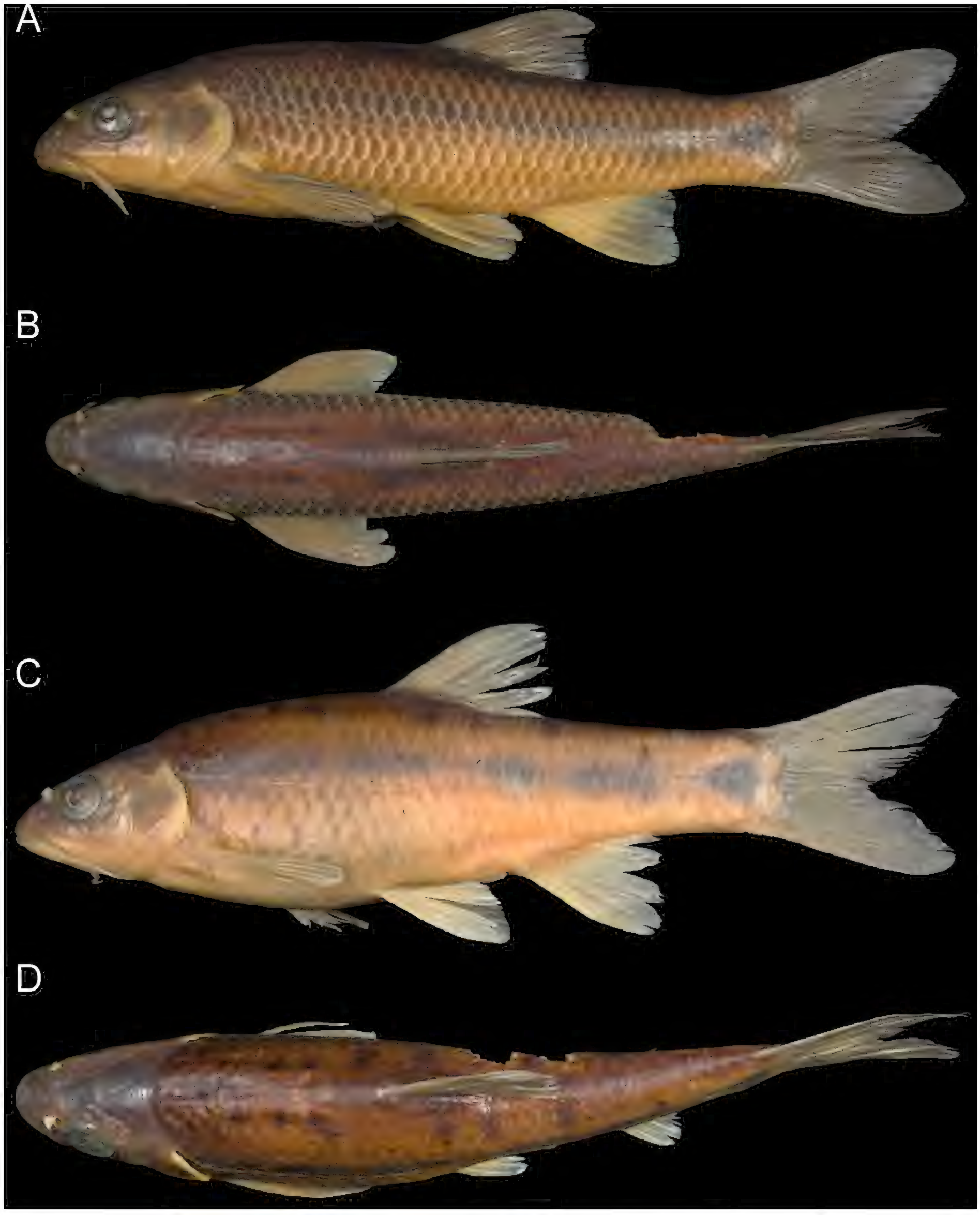

Figure 8. *Pseudobarbus vulneratus*, **A, B.** SAIAB 246286 (tag number X19), male, neotype, 67.3 mm SL, Breede River system; **C, D.** SAIAB 200995 (tag number X26), 69.5 mm SL, Breede River system.

the Baviaans River at Genadendal in the Breede River system—as a definitive reference for *P. vulneratus*. The neotype, SAIAB 246286 (male, 67.3 mm SL; Fig. 8A, B), was selected from well-preserved, recently collected material.

Neotype. • SAIAB 246286 (tag number X19), male, 67.3 mm SL, Baviaans River at Genadendal, Breede River system, South Africa, -34.026972, 19.5558, collected by A. Chakona & J. Merron, 2 March 2009.

Additional material (n = 55). • SAIAB 201149 (tag numbers X18 and X20–X21), 3 specimens, 65.9–70.9 mm SL, Baviaans River at Genadendal, Breede River system, South Africa, -34.026972, 19.5558, collected

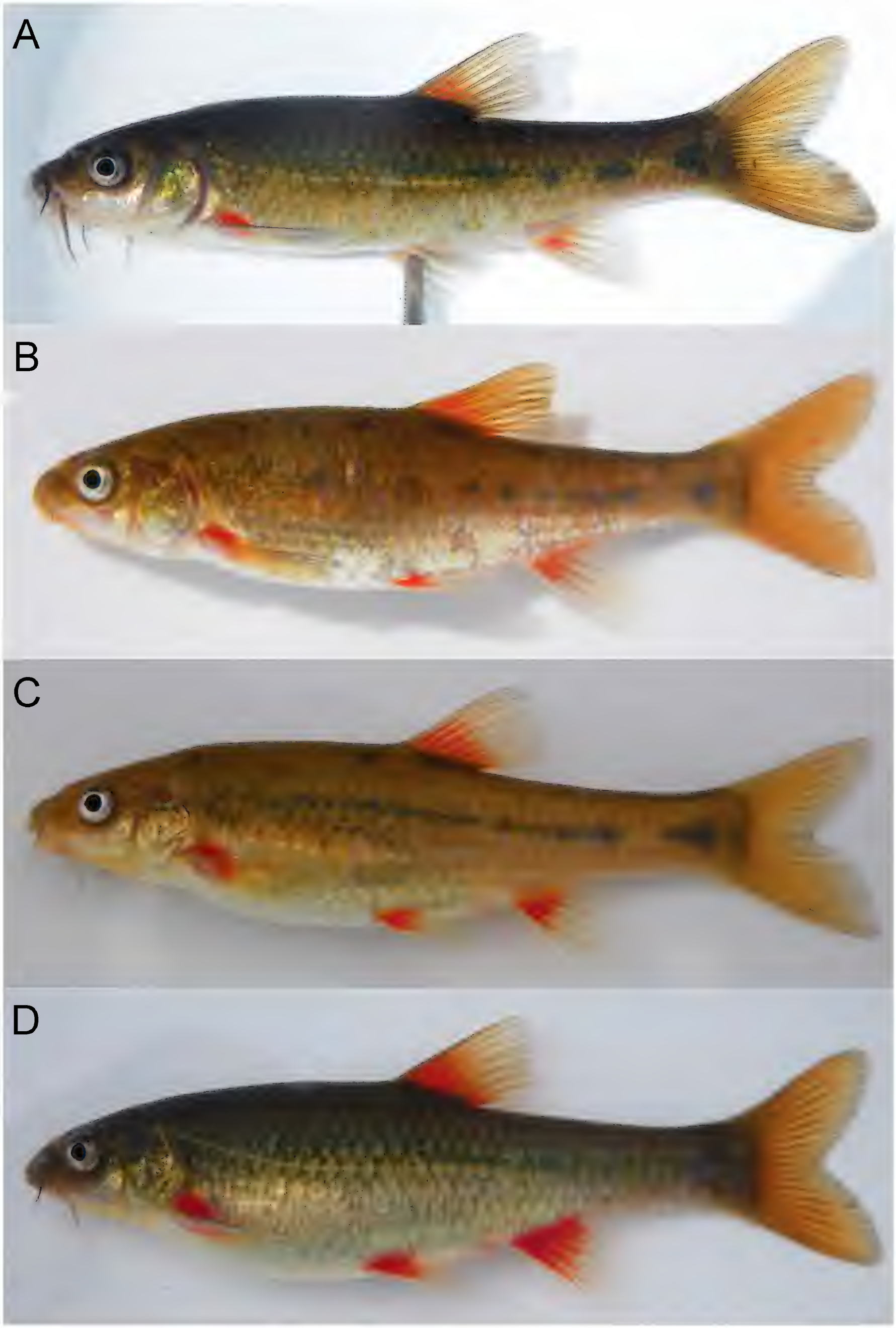

Figure 9. Fresh specimens of *Pseudobarbus vulneratus* from the **A.** Goukou River (SAIAB 209807); **B.** Melkhoutrivier near Malgas, Breede River system (SAIAB 210452); **C.** Koringlandsrivier at Swellendam, Breede River system (SAIAB 210023), and **D.** Riviersonderend, Breede River system (SAIAB 209790).

by A. Chakona & J. Merron, 2 March 2009. • SAIAB 210452 (tag numbers X11–X17), 7 specimens, 62.1–70.5 mm SL, Melkhout River, Breede River system, South Africa, -34.370527, 20.6456, collected by A. Chakona & J. Merron, 28 September 2009. • SAIAB 200995 (tag numbers X22–X28), 7 specimens, 51.1–89.4 mm SL, Gobos River at Greyton, Breede River system, South Africa, -34.03638, 19.62575, collected by A. Chakona & E. Swartz, 5 March 2009. • SAIAB 210457 (tag numbers X29–X32), 4 specimens, 63.6–75.0 mm SL, Duiwenhok River, South Africa, -34.00705, 20.88383, collected by A. Chakona & W. Kadye, 1 October 2009. • SAIAB 209918 (tag numbers X33–X36), 4 specimens, 54.8–69.7 mm SL, Amandel River, Breede River system, South Africa, -33.50661, 19.494972, collected by A. Chakona & E. Swartz, 7 December 2008. • SAIAB 193378 (tag numbers X37–X40), 4 specimens, 47.0–61.0 mm SL, Willem Nels River, Breede River system, South Africa, -33.7583, 19.875, collected by E. Swartz & H. Roos, 19 March 2001. • SAIAB 193373, 3 specimens, 55.7–61.6 mm SL, Melkhout River, Breede River system, South Africa, -34.36, 20.638, collected by E. Swartz & H. Roos, 17 March 2001. • SAIAB 210019, 2 specimens, 62.0–67.5 mm SL, Keurbooms River, Breede River system, South Africa, -33.98561, 20.373, collected by A. Chakona & W. Kadye, 7 October 2009. •SAIAB 201128, 2 specimens, 51.6–53.9 mm SL, Titus River, Breede River system, South Africa, -33.4053, 19.41805, collected by A. Chakona & E. Swartz, 22 February 2009. • SAIAB 193816, 2 specimens, 64.7–66.8 mm SL, Twee, Breede River system, South Africa, -33.6, 19.32361, collected by E. Swartz & H. Roos, 23 March 2001. • SAIAB 186076, 2 specimens, 56.1–67.2 mm SL, Duiwenhoks River, South Africa, -33.97839, 21.03233, collected by E. Swartz & W. Bronaugh, 9 March 2012. • SAIAB 130671, 3 specimens, 40.1–42.5 mm SL, Baviaans River at Genadendal, Breede River system, South Africa, -34.0325, 19.55861, collected by S. Thorne, 9 December 1986. • SAIAB 209991, 2 specimens, 54.2–58.4 mm SL, Duiwenhoks River, South Africa, -34.019638, 20.93455, collected by A. Chakona. • SAIAB 209799, 5 specimens, 58.6–70.9 mm SL, Goukou River, South Africa, -34.017194, 21.290583, collected by A. Chakona & J. Merron, 7 April 2009. • SAIAB 209807, 5 specimens, 67.4–81.2 mm SL, Goukou River, South Africa, -33.984916, 21.20716, collected by A. Chakona & J. Merron, 9 April 2009.

Diagnosis. *Pseudobarbus vulneratus* can be distinguished from all currently recognised congeners by the following combination of character states: subterminal mouth with two pairs of barbels; circumpeduncular scale count of 12–13; predorsal scale rows of 14–18 (usually 15–16); head length 24.2–29.8% SL; anterior barbel 6.8–31.2% HL; orbit diameter 18.1–27.2% HL; absence of linear body stripes; presence of dorsal and mid-lateral spots and blotches; tuberculation in mature breeding males (large to small conical/blunt tubercles, 1–6 in each snout cluster, single row above each naris with 1–3 tubercles per cluster, single row above each orbit with 1–5 tubercles per cluster); and 2 teeth in the outer pharyngeal tooth row. Additionally, *Pseudobarbus vulneratus* is distributed across the Breede River system (excluding the Huis and Tradouw catchments), as well as the Duiwenhoks and Goukou river systems.

Description. All morphometric values in the text are presented with the neotype value first, followed by any differing values for additional material in parentheses.

General morphology. See Table 3 for body proportions and meristics. Body moderately elongate, fusiform and laterally compressed; dorsal profile more convex than ventral profile; greatest depth anterior to dorsal fin origin 4.2 (3.6–5.0) in SL. Caudal peduncle depth 0.5 (0.4–0.6) times its length. Large head, length 3.7 (3.4–4.2) in SL, depth at eye 6.6 (6.0–7.8) in SL and 0.6 (0.5–0.7) times greatest body depth. Dorsal profile of head posterior to orbit steep. Snout short and oblique, convex, its length 1.8 (1.1–2.0) times eye diameter and 2.6 (2.5–3.9) in head length. Large eyes, diameter 4.5 (3.7–5.6) in head length, dorsolaterally placed, not extending above the dorsal outline. Interorbital width 1.6 (1.1–2.0) of orbit diameter. Mouth sub-terminal and sickle-shaped, with two pairs of well-developed barbels. Anterior barbel 0.9 (0.3–1.3) times eye diameter, significantly short of anterior eye margin to reaching the middle of the eye. Posterior barbel 1.4 (0.3–2.0) times orbit diameter, ends between posterior edge of pupil and slightly beyond preopercular margin.

Tuberculation. Mature breeding males with conical/blunt tubercles of different sizes on snout and top of head (Fig. 6). Bilateral clusters of large to small tubercles present on snout (1–6 tubercles per cluster). A row of large to small tubercles (similar to snout tubercles in size and shape) extends in an arc above each naris (1–3 tubercles per cluster) to the anterodorsal edge of the orbit and then continues posteriorly with single row of 1–5 tubercles (anteriorly larger) along the dorsal edge of each orbit. Anterior and posterior dorsal clusters, either naked or usually with a few small to tiny tubercles, progressively decrease in size toward the posterior. Scales naked or with a line of minute tubercles along the free edge, except for ventral scales anterior to pelvic fin origin. Scattered minute tubercles may also occur on some scales. Lines of minute tubercles present on fin rays (except caudal fin).

Scales. LL 32–39 (neotype: 36; other material: 32:6, 33:6, 34:11, 35:12, 36:7, 37:4, 38:7, 39:2), LD 5–7 (neotype: 6; other material: 5:3, 6:31, 7:21), LP 4–6 (neotype: 4; other material: 4:9, 5:35, 6:11), LA 4–6 (neotype: 5; other material: 4:14, 5:34, 6:7), CP 12–13 (neotype: 12; other material: 12:42, 13:9), PDS 14–18 (neotype: 17; other material: 14:7, 15:24, 16:13, 17:8, 18:3). Predorsal and ventral scales embedded and smaller than flank scales. All scales cycloid.

Fins. Dorsal fin rays iv/6–iv/8 (neotype: iv/7; other materials: iv/6:1, iv/7:53, iv/8:1); anal fin rays iv/5; pectoral fin rays 13–15 (neotype: 14; other materials: 13:35, 14:15; 15:5); pelvic fin rays 7–8 (neotype: 8; other materials: 7:1, 8:54); caudal fin branched rays 15–18 (neotype: 17; other materials: 15:2, 16:2, 17:48, 18:3). Dorsal fin

in the centre of the body excluding the caudal fin; origin slightly behind origin of pelvic fin; tip of depressed dorsal fin nearly reaches vertical line at anal fin posterior base or is 0.5–1.5 scales short in both sexes. Pectoral fin fan-shaped, variable in length, reaches/surpasses or short (0.5–3 scales) of pelvic fin origin in both sexes. Pelvic fin origin slightly in front of dorsal fin origin, length variable, tip of depressed pelvic fin reaches/surpasses or 0.5–2 short of anterior anal fin origin in both sexes. Caudal fin forked.

Osteology (n = 17). Vertebral column including Weberian apparatus and urostyle: total vertebrae 34–38 (neotype: 37; other materials: 34:1, 35:1, 36:8, 37:5, 38:1), predorsal vertebrae 11–13 (neotype: 12; other material: 11:4, 12:11, 13:1), precaudal vertebrae 19–21 (neotype: 19; other material: 19:9, 20:5, 21:2), caudal vertebrae 15–18 (neotype: 18; other material: 15:2, 16:3, 17:9, 18:2).

Gill rakers (n = 5): 3–5+1+9–11 (epibranchial: 3:3, 4:1, 5:1; angle: 1:5; ceratobranchial: 9:1, 10:3, 11:1).

Pharyngeal teeth (n = 5). Three rows of pharyngeal teeth, teeth pattern 2,3,4–5 + 4–5,2–3,2. The distribution frequency of pharyngeal teeth is given in Table 4.

Colour of fresh specimens. Refer to Fig. 9 for general live colouration. The colouration of the species varies from light to dark olive green or golden brown, with larger specimens tending to be darker. The dorsal surface of the head and body is typically darker, while the ventral surface is lighter. A mid-lateral band may be present, though it can be either distinct or indistinct. The dorsal half of the body is often marked by large dark spots and blotches, including a series of irregular spots along the mid-lateral line and a prominent triangular or sub-triangular marking at the end of the caudal peduncle. The basal half of the fins is scarlet, with dark brown fin rays, and the distal membranes are hyaline.

Colour of preserved specimens. Refer to Fig. 8 for colouration of preserved specimens. A distinct mid-lateral band ending in the form of a triangular mark anterior to the base of the caudal fin usually present. Dorsal head and body dark or dark brown, fading to lighter below. A mid-lateral series of irregular blotches and spots over the dorsal half of the body usually present. Blotches and spots may be absent in some larger specimens or breeding males with conical tubercles on heads.

Distribution and ecology. *Pseudobarbus vulneratus* has a relatively wide geographical range, as it occurs across the Breede, Duiwenhoks and Goukou River systems (Fig. 2; Swartz et al. 2009, 2014; Chakona et al. 2013). It has been known to inhabit boulders and bedrock pools with deep flowing stretches of larger tributary streams and mainstreams. As a bottom feeder, it feeds on detritus and small organisms. Breeding season occurs during summer, where males have been recorded to generate sounds (Lowe and Skelton 2008).

Conservation. This lineage has been classified in the IUCN Red List Assessment of South African freshwater fish as Vulnerable (VU) (Chakona et al. 2022). According to Skelton (2024), the large reduction in the population range of this lineage is due to destroyed habitats for the development of townships and large-scale agriculture, industries that abstract or divert water, pollution, invasive riparian plants, and introduced alien predatory fishes, particularly bass and trout.

Etymology. Castelnau (1861) did not clarify the origin or reasoning behind the specific name. The gender-correct scientific name is *Pseudobarbus vulneratus*, as the genus is masculine.

Comparison with other species

Pseudobarbus vulneratus can be readily identified from *P. afer*, *P. asper*, *P. kubhekai*, *P. phlegethon*, *P. quathlambae*, *P. senticeps*, *P. swartzi*, and *P. tenuis* by its two pairs of oral barbels, in contrast to the single pair found in the others. *Pseudobarbus vulneratus* differs from *P. skeltoni* in circumpeduncular scale count (12–13, usually 12 vs. 15–18, usually 16–17), predorsal scale count (14–18, usually 15–16 vs. 17–21, usually 18–19), maximum body length (89.4 vs. 163.4 mm SL), head length (24.2–29.8 vs. 28.5–35.6% SL), mouth morphology (subterminal in all size classes vs. terminal in adults), tuberculation of head in mature breeding males (large to small conical/blunt tubercles, 1–6 in each snout cluster, single row above each naris with 1–3 per cluster, and single row above each orbit with 1–5 per cluster vs. large prominent conical tubercles, 22–30 in each snout cluster, multiple rows above each naris with 6–16 per cluster, and multiple rows above each orbit, with up to 12 per cluster; Fig. 6), and distribution (Breede, Duiwenhoks and Goukou river systems vs. upper Riviersonderend River, a major tributary of the Breede River, and Krom River, a tributary of the Molenaars River in the Breede River system). *Pseudobarbus vulneratus* differs from *P. burgi* in anterior barbel length (6.8–31.2 vs. 0.9–9.1% HL, present only in specimens larger than 40 mm SL), tuberculation of head in mature breeding males (large to small conical or blunt tubercles, 1–6 in each snout cluster vs. large conical tubercles, 10–15 in each snout cluster), absence of linear stripes on the body above and below the mid-lateral band (vs. present, Fig. 7), and distribution (Breede, Duiwenhoks and Goukou river systems vs. Great Berg River system and formerly the Eerste River). *Pseudobarbus vulneratus* differs from *P. verloreni* in anterior barbel length (6.8–31.2% HL vs 6.3% HL for the holotype and 3.3 ± 0.3% HL for the paratypes), orbit diameter (18.1–27.2 vs. 31.2% HL for the holotype and 31.5 ± 0.4% HL for the paratypes), absence of linear stripes on the body above and below the mid-lateral band (vs. present, Fig. 7), presence of dorsal and mid-lateral spots and blotches (vs. absent), tuberculation of head in mature breeding males (large to small conical or blunt tubercles, 3–10 in each snout cluster vs. tubercles confined to snout with 2 in each cluster), and distribution (Breede, Duiwenhoks and Goukou river systems vs. Verlorenvlei River system). *Pseudobarbus vulneratus* and *P. burchelli* differ in circumpeduncular scale count and distribution. *Pseudobarbus vulneratus* differs

from its closest relative, *P. agulhas* sp. nov., in circumpeduncular scale count (12–13 vs. 14–16, usually 15) and distribution (Breede, Duiwenhoks and Goukou river systems vs. Heuningnes and Klein River systems).

Pseudobarbus agulhas Zarei, Martin & Chakona, sp. nov.

https://zoobank.org/2EF16BE2-E530-437C-9AEF-9D0CD4927DA6

English name: Agulhas redfin

Afrikaans name: Agulhas-rooivlerkie

Figs 10, 11

Type materials. ***Holotype.*** • SAIAB 246287 (tag number H1), 69.9 mm SL, Grashoek River, Heuningnes River system, South Africa, -34.579194, 19.967305, collected by A. Chakona, N. Mazungula & X. Mathebula, 21 February 2024.

Paratypes (n = 19). • SAIAB 237284 (tag numbers H2–H9), 8 specimens, 46.4–80.4 mm SL, same data as for holotype. • SAIAB 246289 (tag numbers X72–X78), 7 specimens, 59.6–65.7 mm SL, Grashoek River, Heuningnes River system, South Africa, -34.590769, 19.994032, collected by J. Martens, Abraham & S. Thorne, 24 March 1983. • SAIAB 201020 (tag numbers X68–X71), 4 specimens, 45.6–50.4 mm SL, Grashoek River, Heuningnes River system, South Africa, -34.574, 19.948, collected by A. Chakona & E. Swartz, 18 February 2009.

Additional material (n = 15). • SAIAB 246288 (tag numbers X52–X67), 15 specimens, 52.7–88.1 mm SL, Karingmelksriver, Klein River System, South Africa, -34.395137, 19.709277, collected by A. Chakona, A. Anderson, M. Mtshintshi, S. Anele Ngema & N. Khusi, 20 & 21 December 2023.

Diagnosis. *Pseudobarbus agulhas* sp. nov. can be distinguished from all other known species in the genus through the following set of characters: subterminal mouth with two pairs of barbels; 14–16, usually 15 scale rows around the caudal peduncle; 15–18, usually 16–17 predorsal scales; lateral line to dorsal fin scales 6–8, usually 6–7; 19–21, usually 20 precaudal vertebrae; 14–16 pectoral fin rays; interorbital width 32.3–38.7% HL; anterior barbel length 8.4–24.8% HL; orbit diameter 18.4–26.4% HL; absence of linear stripes on the body; presence of dorsal and mid-lateral spots and blotches; tuberculation of head in mature breeding males: large to small conical/blunt tubercles, 3–4 in each snout cluster, single row above each naris with 0–3 tubercles per cluster, and single row above each orbit with 1–2 tubercles in each cluster; and 0–2, usually 1 tooth in the outer pharyngeal tooth row. Additionally, *Pseudobarbus agulhas* sp. nov. is the sole redfin species found in the Heuningnes and Klein River systems.

Description. All morphometric values in the text are listed with the holotype first, followed by paratypes and additional materials in parentheses if they differ.

General morphology. Body proportions and meristics are given in Table 3. Body moderately elongate, fusiform, with dorsal profile generally more convex than ventral profile, maximum body depth 4.0 (3.6–4.5) in SL, body laterally compressed. Caudal peduncle shallow, its depth 0.5 (0.4–0.7) times its length. Head long, length 3.6 (3.2–3.9) in SL, depth at eye 6.7 (5.1–7.5) in SL and 0.6 (0.5–0.8) times maximum body depth. Postorbital profile steep. Snout short, oblique, convex, longer than eye, length 1.7 (1.2–1.9) times eye diameter and 2.8 (2.7–3.3) in head length. Eye diameter 4.7 (3.8–5.4) in head length, and dorsolateral, not extending above dorsal profile. Interorbital wide and flat, 1.8 (1.3–2.0) times orbit diameter. Mouth sub-terminal, sickle-shaped, its corner reaching vertical through middle of nares. Mouth with two pairs of well-developed barbels; anterior barbel length 0.8 (0.4–1.3) times orbit diameter, ranging from significantly short of anterior eye margin to extending to the eye midpoint. Posterior barbel length 1.5 (0.9–2.1) times eye diameter, ending between the pupil and slightly beyond preopercular margin.

Tuberculation. Adult breeding males typically with few conical or blunt tubercles of various sizes on their snouts and the tops of their heads (Fig. 6). Bilateral clusters of tubercles, ranging from large to small (3–4, usually 3), are found on the snout. A row of tubercles, varying in size from large to small and resembling those on the snout, extends above each naris (0–3, usually 1–2 per cluster) to the anterodorsal edge of the orbit. A single row of 1–2 tubercles (usually 2, with the anterior one being larger) along the dorsal edge of each orbit. The anterior dorsal area is typically naked but may include a few small or tiny tubercles. The posterior dorsal area is either naked or has a few scattered tiny tubercles. Minute tubercles are present either as a line along the free edges of the scales or scattered across the surface of the body scales located above the lateral line. Lines of minute tubercles are found on the fin rays, though they are less prominent on the caudal fin rays.

Scales. LL 34–39 (holotype: 37; other material: 34:3, 35:5, 36:8, 37:7, 38:7, 39:3), LD 6–8 (holotype: 7; other material: 6:16, 7:17, 8:1), LP 4–6 (holotype: 4; other material: 5:32, 6:2), LA 4–6 (holotype: 4; other material: 4:2, 5:27, 6:5), CP 14–16 (holotype: 15; other material: 14:9, 15:20, 16:4), PDS 15–18 (holotype: 15; other material: 15:4, 16:15, 17:11, 18:3). Predorsal scales and ventral scales between pectoral fin origin and pelvic fin origin embedded and smaller than flank scales. Triangular area between the gill cover and anterior base of pectoral fin naked or scaled.

Fins. Dorsal fin rays iv/7–iv/8 (holotype: iv/7; other materials: iv/7:32, iv/8:2); anal fin rays iv/5–iv/6 (holotype: iv/5; other materials: iv/5:33, iv/6:1); pectoral fin rays 14–16 (holotype: 14; other materials: 14:20; 15:13; 16:1); pelvic fin rays 8–9 (holotype: 8; other materials: 8:32, 9:2); caudal fin branched rays 17–18 (holotype: 17; other materials: 17:33, 18:1). The dorsal fin is positioned nearly at the centre of the body (excluding the caudal fin), with its origin slightly behind the vertical line through the pelvic fin's origin. The distal margin is straight to slightly concave, and in tubercled specimens, the tip of the depressed dorsal fin nearly reaches the vertical line at the posterior base of the anal fin; in other specimens, it falls 0.5–1.5 scales short of that point. The pectoral fin is fan-shaped and varies in length, extending to or beyond the origin of the pelvic fin in tubercled specimens; in other

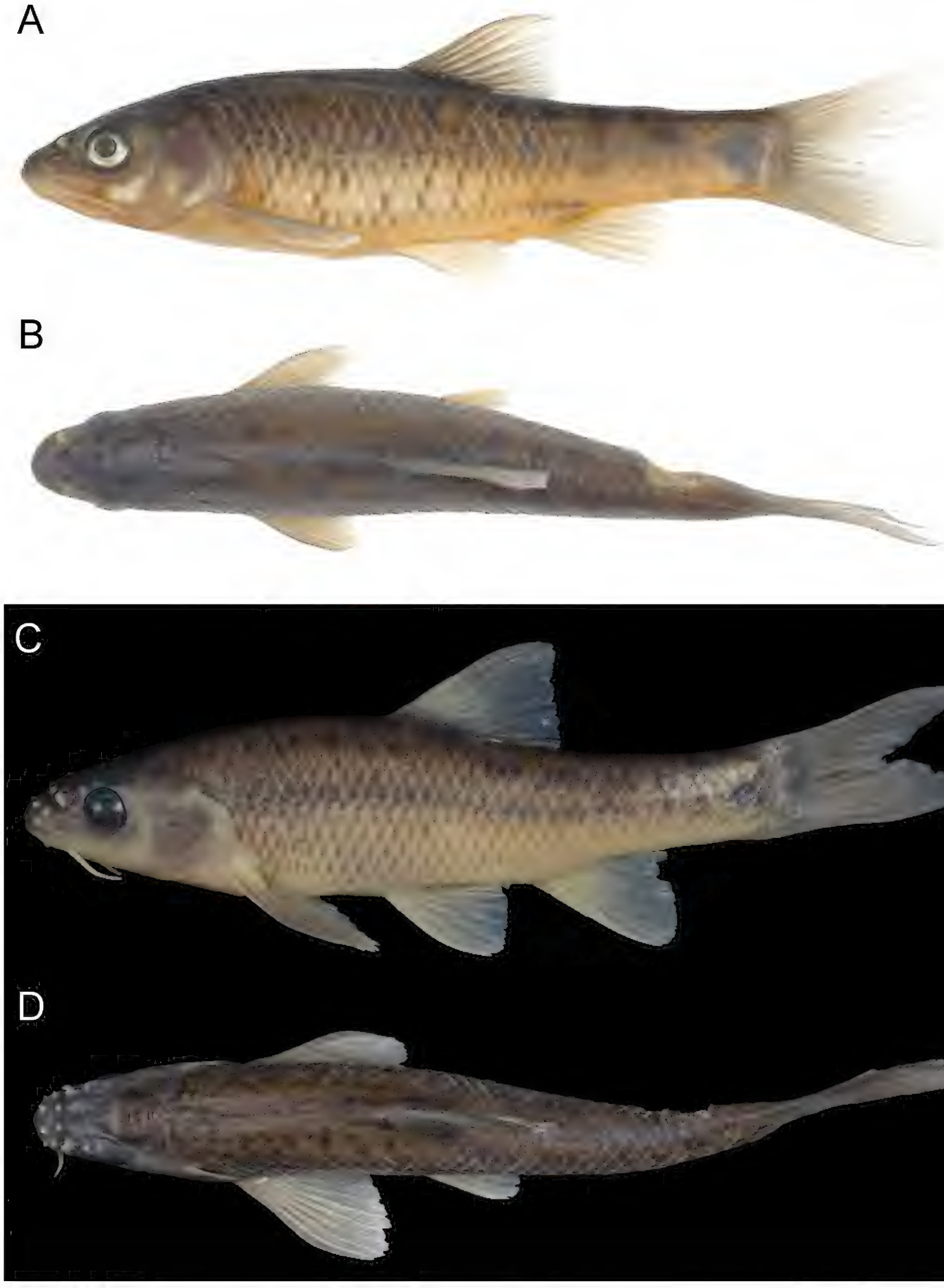

Figure 10. *Pseudobarbus agulhas* sp. nov., **A, B**. SAIAB 246287, holotype, 69.9 mm SL, Grashoek, Hueninghes River system; **C, D**. SAIAB 246288, 88.1 mm SL, Klein River system.

specimens, it falls 0.5 to 2 scales short of the pelvic origin. The origin of the pelvic fin is slightly ahead of the dorsal fin origin, with variable length. The tip of the depressed pelvic fin either reaches or exceeds the anal fin origin or is 0.5 to 3 scales short in both sexes. The distal margin of the anal fin is nearly straight to slightly convex, with its origin located nearer to the origin of the pelvic fin than to the base of the caudal fin. The caudal fin is forked.

Figure 11. Live specimens of *Pseudobarbus agulhas* sp. nov. from the Grashoek River, Heuningnes River system. **A.** SAIAB 246287, holotype, 69.9 mm SL; **B.** SAIAB 237284 (tag H7), paratype, 51.0 mm SL; **C.** SAIAB 237284 (tag H3), paratype, 77.4 mm SL.

Osteology (n = 16). Vertebral column including Weberian apparatus and urostyle: total vertebrae 36–37 (holotype: 37; other materials: 36:6, 37:9), predorsal vertebrae 11–12 (holotype: 11; other material: 11:8, 12:7), precaudal vertebrae 19–21 (holotype: 19; other material: 19:3, 20:11, 21:1), caudal vertebrae 16–18 (holotype: 18; other material: 16:5, 17:9, 18:1).

Gill rakers (n = 5): 3–4+1+10–12 (epibranchial: 3:1, 4:4; angle: 1:5; ceratobranchial: 10:2, 11:2, 12:1).

Pharyngeal teeth (n = 5). Three rows of pharyngeal teeth, teeth pattern 1–2,3,4–5 + 4,2–3,0–1. The distribution frequency of pharyngeal teeth is given in Table 4.

Colour of live specimens. Refer to Fig. 11 for general live colouration. The dorsal surface of the body, above the lateral line, is olive-brown, becoming darker toward the dorsal region. Below the lateral line, the body is marked with blemished silvery-white, gradually transitioning to white on the ventral surface. The base of the fins is bright scarlet, with the colour becoming less pronounced in the caudal fin. The mid-lateral band is indistinct, while a large triangular mark is located at the base of the caudal fin. The dorsum is adorned with sooty dark brown spots and blotches, and

a series of irregular spots may also be visible along the posterior half of the body.

Colour of preserved specimens. Refer to Fig. 10 for colouration observed in preserved specimens. The flanks exhibit a distinct or usually indistinct dark mid-lateral band that tapers into a triangular shape at the base of the caudal fin. The dorsal head and body are olive brown or dark brown, fading to a lighter colour ventrally. Typically, there are dark spots and blotches along the flanks and on the dorsal half of the body, including a mid-lateral series of irregular spots. However, in some larger specimens and breeding males with tubercles on their heads, these blotches and spots may be absent.

Distribution and ecology. *Pseudobarbus agulhas* sp. nov. is characterised by a limited distribution, being found exclusively in the Heuningnes and upper sections of the Klein river system (Fig. 2; Swartz et al. 2009, 2014; Chakona et al. 2013). The species is found in pools and streams, with fry and juveniles occurring in large shoals as opposed to the adults collecting in small groups. As omnivores, they feed on algae and small invertebrates. Like *P. vulneratus*, it breeds during summer, spawning in riffles above pools, coexisting with Cape kurper [*Sandelia capensis* (Cuvier, 1829)] and Cape galaxias [*Galaxias zebratus* (Castelnau, 1861)] (Skelton 2024).

Conservation. In the latest IUCN Red List Assessment for South African freshwater fish, this lineage was classified as Endangered (EN) (Chakona et al. 2022). The populations are threatened due to water extractions for domestic and agricultural use, as well as introduced alien fish such as the bluegill (*Lepomis macrochirus* Rafinesque 1819) and bass (*Micropterus* spp.).

Etymology. The specific epithet *agulhas* is derived from Cape Agulhas, the southernmost point of the African continent, where the Atlantic and Indian oceans meet. This name recognises the region's distinct biogeographic boundary and ecological significance, which supports a rich diversity of both marine and freshwater species. The Heuningnes River, the primary habitat and distribution range of the species, is also located within the Agulhas region. A noun in apposition.

Comparison with other species

Pseudobarbus agulhas sp. nov. can be readily distinguished from *P. asper*, *P. tenuis*, *P. afer*, *P. kubhekai*, *P. phlegethon*, *P. senticeps*, *P. swartzi*, and *P. quathlambae* by its two pairs of oral barbels, in contrast to the single pair found in those species. *Pseudobarbus agulhas* sp. nov. differs from *P. skeltoni* in interorbital width (32.3–38.7 vs. 23.9–32.3% HL), pectoral fin rays (14–16, usually 14–15 vs. 13–14), caudal peduncle scale rows (14–16, usually 15 vs. 15–18, usually 16–17), predorsal scale rows (15–18, usually 16–17 vs. 17–21, usually 18–19), maximum body length (88.1 mm SL vs. 163.4 mm SL, largest size of any *Pseudobarbus* species), mouth morphology (subterminal in all size classes vs. terminal in adults), tuberculation of head in mature breeding males (large to small conical or blunt tubercles, 3–4 in each snout cluster, single row above each naris with 0–3 per cluster, and single row above each orbit with 1–2 per cluster vs. large prominent conical tubercles, 22–30 in each snout cluster, multiple rows above each naris with 6–16 per cluster, and multiple rows above each orbit, with up to 12 per cluster; Fig. 6), teeth count in the inner pharyngeal tooth row (4–5, usually 4 vs. 5), teeth count in the outer pharyngeal tooth row (0–2, usually 1 vs. 2), and distribution (Heuningnes and Klein River systems vs. upper Riviersonderend River, a major tributary of the Breede River, and the Krom River, a tributary of the Molenaars River in the Breede River system). *Pseudobarbus agulhas* sp. nov. differs from *P. burgi* in anterior barbel length (8.4–24.8 vs. 0.9–9.1% HL and only present in specimens above 40 mm SL), lateral line to dorsal fin scales (6–8, usually 6–7 vs. 4–6, usually 5), precaudal vertebrae (19–21, usually 20 vs. 17–20, usually 19), tuberculation of head in mature breeding males (large to small conical or blunt tubercles, 3–4 in each snout cluster vs. large conical tubercles, 10–15 in each snout cluster), absence of linear stripes on the body above and below the mid-lateral band (vs. present, Fig. 7), and distribution (Heuningnes and Klein River systems vs. the Great Berg River system and formerly in the Eerste River). *Pseudobarbus agulhas* sp. nov. differs from *P. verloreni* in anterior barbel length (8.4–24.8% HL vs 6.3% HL for the holotype and 3.3 ± 0.3% HL for the paratypes), orbit diameter (18.4–26.4 vs. 31.2% HL for the holotype and 31.5 ± 0.4% HL for the paratypes), absence of linear stripes on the body above and below the mid-lateral band (vs. present, Fig. 7), presence of dorsal and mid-lateral spots and blotches (vs. absent), tuberculation of head in mature breeding males (large to small conical or blunt tubercles, 3–4 in each snout cluster, single row above each naris with 0–3 per cluster, and single row above each orbit with 1–2 per cluster, with small to tiny tubercles on top of head vs. tubercles confined to snout with 2 in each cluster), teeth count in the inner pharyngeal tooth row (4–5, usually 4 vs. 5), teeth count in the outer pharyngeal tooth row (0–2, usually 1 vs. 2), and distribution (Heuningnes and Klein River systems vs. the Verlorenvlei River system). *Pseudobarbus agulhas* sp. nov. differs from *P. burchelli* in having a narrower head (maximum head width 53.1–61.6% HL, head width at eye 43.1–48.9% HL, and head width at mouth corner 29.7–37.3% HL vs. maximum head width 62.4–71.5% HL, head width at eye 49.3–53.9% HL, and head width at mouth corner 37.4–43.6% HL), teeth count in the outer pharyngeal tooth row (0–2, usually 1 vs. 2–3, usually 2), and distribution (Heuningnes and Klein River systems vs. Huis and Tradouw rivers in the Breede River system). *Pseudobarbus agulhas* sp. nov. and *P. vulneratus* differ in circumpeduncular scale count and distribution.

A key to the double-barbeled species of *Pseudobarbus*

1 Presence of linear speckles on the body (rivers flowing into the west coast of South Africa) 2
– Absence of linear speckles on the body (rivers flowing into the south coast of South Africa) 3
2 Dorsal profile of snout round and prominent; snout long, length 36.7–40.7% HL; snout deep, depth at nares 41.7–48.5% HL; check deep, depth 26.1–30.7% HL; head short, length 24.4–25.6% SL; predorsal short, length 49.6–52.8% SL (Berg River system) ..... *P. burgi*
– Dorsal profile of snout almost straight line; snout short, length 28.5–34.8% HL; snout shallow, depth at nares 34.9–40.4% HL; check shallow, depth 22.8–25.6% HL; head long, length 27.1–30.7% SL; predorsal long, length 53.5–56.7% SL (Verlorenvlei River system) ..... *P. verloreni*
3 Circumpeduncular scale rows 12–13 (Breede, Duiwenhoks and Goukou river systems ..... *P. vulneratus*
– Circumpeduncular scale rows 14–18 4
4 Mouth terminal in adults; interorbital narrow, width 23.9–32.3% HL; predorsal scales 17–21, usually 18–19; circumpeduncular scale rows 15–18, usually 16–17; mature breeding males with 22–30 tubercles in each snout cluster, multiple rows above each naris with 6–16 per cluster, and multiple rows above each orbit with up to 12 per cluster (Upper Rivier-sonderend and Krom rivers in the Breede River system) ..... *P. skeltoni*
– Mouth subterminal in all size classes; interorbital wide, width 32.3–38.7% HL; predorsal scales 14–18, usually 15–17; circumpeduncular scale rows 14–16; mature breeding males with 3–10 tubercles in each snout cluster, single row of 0–5 tubercles above each naris and single row of 1–6 tubercles above each orbit 5
5 Head wide: greatest width at operculum 62.4–71.5% HL, at eye 49.3–53.9% HL, and at mouth corner 37.4–43.6% HL; 2–3, usually 2 teeth in the outer pharyngeal tooth row (Huis and Tradouw rivers in the Breede River system) .. *P. burchelli*
– Head narrow: greatest width at operculum 53.1–61.6% HL, at eye 43.1–48.9% HL, and at mouth corner 29.7–37.3% HL; 0–2, usually 1 tooth in the outer pharyngeal tooth row (Heuningnes and Klein River systems) ..... *P. agulhas* sp. nov.

Discussion

Taxonomic and biogeographic implications

In his 1988 revision of the genus *Pseudobarbus*, P.H. Skelton recognised only seven species, namely *P. burchelli*, *P. burgi*, *P. phlegethon*, *P. tenuis*, *P. afer*, *P. asper*, and *P. quathlambae*. However, due to significant morphological variation within each species, further revisions and the identification of additional taxonomic diversity did not occur until two decades later, with the advent of DNA barcoding and the integration of molecular analyses in taxonomic research. One of the most notable findings was the identification of four distinct lineages within *P. afer* (Swartz et al. 2007), two within *P. burgi* and four within *P. burchelli* (Swartz et al. 2009; Chakona et al. 2013), and three within *P. quathlambae* (Swartz et al. 2023). These lineages exhibit deep genetic divergence and are allopatric, occupying distinct river systems. With the exception of two lineages within *P. quathlambae* and the three lineages within *P. burchelli* resolved in the present study, the taxonomy of these lineages has been clarified through the revalidation of previously synonymised names or the description of new species (Chakona and Swartz 2013; Chakona et al. 2014; Chakona and Skelton 2017; Zarei et al. 2025a, b). However, despite their distinct geographical distributions and considerable genetic divergence, these species are morphologically very similar (Skelton 2024). They are differentiated only by a combination of subtle differences in squamation patterns, colouration, barbel length, head proportions, or tuberculation in mature breeding males. This morphological similarity was also observed in the present study. In the *P. burchelli* complex, despite species being distributed across separated river systems and exhibiting substantial evolutionary divergence, morphological differences are minimal. *Pseudobarbus vulneratus* differs from *P. burchelli* and *P. agulhas* in circumpeduncular scale count, while *P. agulhas* and *P. burchelli* vary in head and snout width, as well as in the number of teeth in the outer pharyngeal tooth row. These three species are further supported by results from multiple molecular species delimitation methods, as well as by their long history of isolation, which reflects the complex biogeographic history of the region (see below).

The greatest phylogenetic divergence within the *P. burchelli* complex is between *P. burchelli* in the Tradouw catchment and *P. vulneratus* + *P. agulhas*. Divergence estimates indicate that *P. burchelli* split from *P. vulneratus* + *P. agulhas* during the late Pliocene to early Pleistocene, ca. 1.67 Mya (0.90–2.80 Mya 95% HPD) (Swartz et al. 2014), when elevated sea levels may have fragmented river systems (Siesser and Dingle 1981), isolating freshwater populations and driving allopatric divergence within *P. burchelli* s.l. If lower sea levels alone had reconnected isolated *P. burchelli* s.l. populations, the Breede, Duiwenhoks, and Heuningnes systems would be expected to show recent migration links, with the Goukou population being more divergent. However, this is not the case. While *P. vulneratus* in the Breede and Duiwenhoks systems can be explained by river confluence during lower sea levels of the Last Glacial Maximum (LGM) (Tankard 1976; Rogers 1985; Ramsay and Cooper 2002; Compton 2011; Cawthra et al. 2014), its presence in the Goukou system cannot be attributed to this event. As proposed by Dingle and Rogers (1972) and Birch (1980), the Goukou and Gourits river systems once converged, with the Gourits–Goukou palaeoriver likely flowing southward

across the Agulhas Bank, while the Breede–Duiwenhoks–Heuningnes system flowed southwestward. As a result, these two palaeoriver systems would not have intersected during a period significant to the evolution of *P. burchelli* s.l. A recent river capture between the Duiwenhoks and Goukou systems may explain the presence of *P. vulneratus* in the Goukou and the low divergence from the Breede–Duiwenhoks populations. Similar habitats in these systems may have allowed minimal adaptation, though human-mediated translocation is also a possibility for the species' presence in the Goukou (Swartz et al. 2014).

The southern coastal lowlands now drained by the Heuningnes, Duiwenhoks, and Goukou systems were likely submerged during the early Pliocene transgression. Consequently, the colonisation of the Heuningnes River system by redfins (now *P. agulhas*) occurred after this event. Colonisation of the Heuningnes may have resulted from the confluence of the Breede–Duiwenhoks palaeoriver and the Heuningnes River. However, divergence time estimates, i.e., ca. 0.77 Mya (0.25–1.30 Mya 95% HPD) (Swartz et al. 2014), suggest that the separation between *P. vulneratus* and *P. agulhas* occurred before the LGM regression, indicating that isolation happened earlier. This raises the possibility that the Heuningnes and Breede–Duiwenhoks palaeorivers never confluented before the –130 m LGM sea level and that redfins reached the Heuningnes by alternative mechanisms. Following colonisation and divergence, ecological differences between the Heuningnes and Breede systems may have prevented lineage exchange. The Heuningnes system has higher conductivity, increased turbidity, and lower gradients than Breede tributaries, which may explain the current distribution. Habitat preferences could account for the separation of lineages despite a potential LGM connection. Alternatively, waterfalls in the offshore reaches between the Heuningnes and Breede–Duiwenhoks palaeorivers may have acted as barriers to dispersal (Swartz et al. 2014).

The deep divergence between *Pseudobarbus burchelli* and *P. vulneratus* + *P. agulhas* is notable, given the small size of the Tradouw catchment. A waterfall prevents upstream gene flow, and while downstream migration may have occurred, no mtDNA introgression has been detected (Chakona et al. 2013; Swartz et al. 2014). It is surprising that *P. burchelli* did not expand its range within the Breede River system. This suggests either that *P. burchelli* never came into contact with *P. vulneratus* or that the two remained reproductively isolated. This may reflect competition avoidance or ecological gradients, although further research is required to compare the ecological traits of *P. burchelli* and *P. vulneratus*.

Previous research on the biology and ecology of *Pseudobarbus burchelli* s.l. provides limited insight, owing to the recent discovery of cryptic diversity within the species. Consequently, it remains unclear which specific lineage or species was the focus of earlier studies by Esterhuizen (1978), De Vos (1989), and Cambray and Stuart (1985). While the reproductive biology of the three species in this complex remains undocumented, it is likely that spawning occurs from October to December, as indicated by the presence of prominent tubercles in males observed during field surveys. Further studies are needed to investigate the habitat preferences, feeding ecology, and reproductive biology of this species complex.

Conservation status and threats

In recent IUCN Red List assessments, Chakona et al. (2022) evaluated the conservation status of *Pseudobarbus* species and lineages in South Africa. Chakona et al. (2022) classified the *P. burchelli* 'Tradouw' lineage (=*P. burchelli*) as Critically Endangered (CR), the *P. burchelli* 'Breede' lineage (=*P. vulneratus*) as Vulnerable (VU), and the *P. burchelli* 'Heuningnes' lineage (=*P. agulhas*) as Endangered (EN). These assessments highlight the ongoing concerns over the conservation of these species. The primary threats to the Barrydale Redfin (*P. burchelli*) include its limited distribution and small population size, habitat loss, the impact of alien invasive species, and reduced genetic diversity (Swartz et al. 2014; Jordaan et al. 2016, 2024; Ellender et al. 2017; Chakona et al. 2022, 2024). Currently, *P. burchelli* is split into two primary subpopulations that persist throughout the dry season: one in deep pools above a causeway in the upper Huis River and another in the lower Tradouw River, within Tradouw's Pass. A smaller subpopulation exists in the upper Tradouw River, but it is unlikely to be viable due to small numbers of adult individuals and the threat posed by non-native fish and agricultural impacts. During the rainy season, these subpopulations reconnect when water flow resumes (Chakona et al. 2024; Jordaan et al. 2024). Historically, the Huis River had perennial flow, but complete water abstraction above the Huis Waterfall has transformed it into an intermittent river, which recedes into isolated pools during the dry season. These pools are unstable, sometimes persisting throughout the dry season, while in other years they dry up completely depending on drought intensity. This fluctuation causes extreme habitat variability, leading to significant population fluctuations. Complete surface water abstraction, poor management of riparian zones, and degradation of river structure due to poor land-use practices—such as instream bulldozing—have all contributed to habitat destruction. Extensive bulldozing occurs upstream of Barrydale in the Huis River, although the area above the causeway remains unaffected and has been identified as a potential sanctuary for the species. However, total water abstraction above the town's extraction point has rendered much of the upper Huis River dry, except for a few isolated pools below the waterfall. The lower Tradouw River, downstream of Barrydale, is significantly impacted by nutrient pollution from sewage effluent and potential agrichemical runoff. Additionally, water abstraction for agriculture in the upper Tradouw River exacerbates habitat degradation. Monitoring between 2012 and 2016 has revealed a progressive increase in alien fish abundance,

with *Pseudobarbus burchelli* now absent from sections of the river where alien species are prevalent. Surveys have also shown a decline in the number of mature individuals and a contraction of the species' historical range due to local extinctions in areas invaded by non-native fish (Jordaan et al. 2024). Despite the lack of studies specifically addressing the effects of pollution on *P. burchelli*, the presence of alien fish species such as Largemouth Bass [*Micropterus nigricans* (Cuvier, 1828)], Banded Tilapia (*Tilapia sparrmanii* Smith, 1840), and Bluegill Sunfish (*Lepomis macrochirus* Rafinesque, 1819) has been well documented (Chakona and Swartz 2013; Chakona et al. 2024; Jordaan et al. 2024). Preliminary surveys suggest that *P. burchelli* have been locally extirpated from pools invaded by Largemouth Bass and Bluegill Sunfish, while Banded Tilapia may compete with the redfin for resources. A Biodiversity Management Plan for Species (BMPS), guided by national norms and standards for conservation planning, is currently being developed to improve the conservation status of *P. burchelli* by increasing its area of occupancy and protecting critical habitats (Jordaan and Villiers 2016; Jordaan et al. 2016). The plan outlines several key objectives, including research and monitoring, preventing habitat loss, stakeholder engagement, and mitigation of alien species. Specific actions to achieve these objectives, as well as strategies for successful implementation, are being defined through a consultative stakeholder process (Jordaan et al. 2016). There is a need to implement measures to control both point and diffuse sources of pollution, as well as manage alien fish species in the catchment. Additionally, further studies are required to determine the ecological flow requirements needed to support the recovery of the Barrydale Redfin.

The historical isolation processes that have led to the divergence of *P. burchelli*, *P. vulneratus*, and *P. agulhas* must be preserved to ensure their continued evolutionary trajectory. This can be achieved by maintaining their geographical isolation and protecting the distinct habitats in which they occur. The limited differentiation observed within *P. burchelli* and *P. vulneratus* suggests a history of, and ongoing, gene flow, which should be actively maintained (Swartz et al. 2014). In the case of *P. vulneratus*, restoring corridors between the currently isolated populations may present challenges, particularly due to geographic and ecological barriers. Nonetheless, records from the South African Institute for Aquatic Biodiversity (SAIAB) collection, along with results by Swartz et al. (2014) and Chakona et al. (2013), indicate that multiple populations of *P. vulneratus* are distributed across the Breede, Duiwenhoks, and Goukou river systems. If these populations are sufficiently large, they can help prevent local inbreeding and maintain genetic diversity within each system. In contrast to *P. burchelli* and *P. vulneratus*, *P. agulhas* is characterised by two sublineages with relatively shallow divergence. One sublineage was recently identified in the Karingmelksriver, representing the species' sole population within the Klein River System. The second sublineage, which likely has an evolutionary history in the Heuningnes River system, has also recently expanded into the Karingmelksriver, potentially through natural dispersal via river connectivity or human-mediated activities (Figs 1, 2). Accordingly, *P. agulhas* should be considered as comprising two distinct management units (MUs; Moritz 1994, 1999): one in the Karingmelksriver (within the Klein River System) and the other in the Heuningnes River System. Each unit requires independent monitoring and management. For instance, if the Karingmelksriver population is overexploited or extirpated due to human activities or other factors, it cannot be restored by translocating individuals from the Heuningnes River system, as these represent separate MUs and sublineages.

An emerging threat to the three species of the *P. burchelli* complex is the infestation of some populations with black spot disease, caused by diplostomid metacercaria (Digenea: Diplostomidae). This parasitic infection is characterised by the presence of small black cysts on the skin, fins, and gills of the affected fish (Bush et al. 2001; Lane and Morris 2010). Black spot disease, which is often linked to poor water quality and habitat degradation, can weaken the health of infected individuals by increasing physiological stress, reducing growth rates, and impairing reproductive success (Hoole et al. 2001). In this study, black spot disease was observed to affect populations of *P. agulhas* more extensively in the Heuningnes River system, with notable incidences also recorded in *P. burchelli* (Jordaan et al. 2024). The presence of diplostomid parasites may also indicate broader ecosystem imbalances, such as an overabundance of snails, which serve as intermediate hosts for the parasite. This may often be linked to poor environmental conditions or altered habitat structure. As a result, the black spot disease adds an additional layer of risk to the conservation of redfin species in the *P. burchelli* complex, compounding the existing threats of habitat loss and invasive species.

Other material examined for morphology

Pseudobarbus afer (Peters, 1864): SAIAB 34422, 5 males (44.9–65.5 mm SL), 5 females (59.2–74.5 mm SL), Blindekloof River, Groendal Wilderness, Swartkops River system, South Africa, collected by D. Boulle and P.H. Skelton, 11 November 1988. SAIAB 34428, 5 unsexed, 60.1–75.1 mm SL, Blindekloof River, Groendal Wilderness, Swartkops River system, South Africa, collected by D. Boulle, 8 June 1989. SAIAB 121688 (formerly AMG 2524), 24 unsexed, 46.0–81.0 mm SL, Elands River, Swartkops River system, South Africa, -33.7667, 25.1278, collected by P.H. Skelton and A. Bok, 5 September 1974. SAIAB 119909 (formerly AMG745), 5 unsexed, 46.0–61.0 mm SL, Elands River, Swartkops River system, South Africa, -33.71667, 25.1000, collected by R.A. Jubb, 15 February 1964. SAIAB 119773 (formerly AMG 609), 30 unsexed, 48.5–66.5 mm SL, Wit River, Sundays River system, South Africa, -33.3, 25.683, collected by R.A. Jubb,

8 April 1959. SAIAB 119940 (formerly AMP 776), 5 unsexed, 43.0–82.0 mm SL, Kragga Kamma, Baakens River system, South Africa, -33.95, 25.5, collected by D. Bicknell, 15 January 1964.

Pseudobarbus outeniqua Zarei, Bragança, Skelton & Chakona, 2025: SAIAB 237307, 1, male, 67.6 mm SL, Kouma River at Willem's Farm, Klein Brak River system, South Africa, -33.95261111, 21.97691667, collected by A. Chakona, N. Mazungula, and X. Mathebula, 25 February 2024. SAIAB 246084, 14 unsexed, 46.6–81.7 mm SL, Kouma River at Willem's Farm, Klein Brak River system, South Africa, -33.95261, 21.97691667, collected by A. Chakona, N. Mazungula, and X. Mathebula, 25 February 2024. SAIAB 128708, 5 unsexed, 50.1–67.4 mm SL, Causeway at Kruisvallei/George, Keurbooms, South Africa, -33.812, 23.17472, collected by J. Olivier and S. Thorne, 01 March 1983. SAIAB 200541, 2 unsexed, 74.9–86.9 mm SL, Kwaai River, Keurbooms, South Africa, -33.82, 23.17972, collected by E. Swartz, 11 April 2000. SAIAB 128186, 3 unsexed, 48.6–52.6 mm SL, Kaapsedrif, Tsitsikamma, South Africa, -34.16, 24.4, collected by A.H. Bok and M. King, 12 May 1982. SAIAB 64260, 1 unsexed, 68.0 mm SL, Tsitsikamma National Park, Groot River, South Africa, collected by I.A. Russel, 26 February 2001. SAIAB 122981, 1 unsexed, 47.7 mm SL, Palmietvlei road at Kaapsedrif, Tsitsikamma, South Africa, -34.05, 24.4, collected by D. Heard, 28 October 1976.

Pseudobarbus burgi (Boulenger, 1911): SAIAB 121240, 28 specimens, 41.80–107.82 mm SL, Wellington, Krom River, Berg River system, South Africa, -33.62861, 19.03916, collected by P. Skelton and C. Gaigher, 9 December 1973. SAIAB 125308, 13 specimens, 25.6–42.0 mm SL, road bridge at entrance to Franchhoek Forestry Station, Franschhoek, Berg River system, South Africa, -33.85, 19.05, collected by S. Thorne, 10 November 1978. SAIAB 128824, 185 specimens, 21.84–48.25 mm SL, bridge of Paleisheuwel road, Endekuil, Kruismans, Berg River system, South Africa, -32.6, 18.75, collected by S. Harmse and S. Thorne, 15 March 1983. SAIAB 130453, 5 specimens, 36.6–60.1 mm SL, Concordia Farm, the bridge towards Piketberg/Elandsbaai road, Kruismans, Berg River system, South Africa, -32.74638, 18.81916, collected by S. Thorne, 17 November 1986. SAIAB 130477, 3 specimens, 73.0–94.8 mm SL, Moravia/Piketberg road, Plaktoof, Berg River system, South Africa, -32.873, 18.67027, collected by S. Thorne, 19 November 1986. SAIAB 130526, 5 specimens, 44.3–100.7 mm SL, Wel van Pas Farm, Krom River, Berg River system, South Africa, -33.62583, 19.08194, collected by S. Thorne, 25 November 1986. SAIAB 186124, 4 specimens, 79.1–92.0 mm SL, about 6.8 km above the Berg River dam wall, Berg River system, South Africa, -33.96185, 19.06893, collected by E. Swartz and W. Bronaugh, 25 February 2012. SAIAB 200355, 5 specimens, 55–68 mm SL, tributary Tierkloof, small tributary above Wemmershoek Dam near Paarl (middle between Drakenteins and Olifants Dam), Berg River system, South Africa, -33.83383, 19.112972, collected by R. Bills, V. Bills and M. Jordan, 19 August 2014.

Pseudobarbus kubhekai Zarei, Mathebula & Chakona, 2025: SAIAB 204589 (tag number F91), holotype, male, 60.5 mm SL, Umzimkulu River system, South Africa, collected by A. Chakona, N. Mazungula, S. Kubheka and N. Ntuli, 25 May 2017. SAIAB 246079 (tag numbers F85–F90 & F92–F94), paratypes, 9 unsexed, 45.9–62.9 mm SL, same locality information and collectors as holotype. SAIAB 246080 (tag numbers F111–F113), paratypes, 3 unsexed, 47.2–78.3 mm SL, same locality information as holotype, collected by P.S. Kubheka and N.S. Ntuli, 26 May 2017.

Pseudobarbus phlegethon (Barnard, 1938): SAIAB 51367, 9 unsexed, 51.7–55.7 mm SL, 3–4 km downstream from Algeria, Rondegat River, Olifants System, South Africa, -32.34999847, 19.0333003998, collected by R. Bills, D. Impson and M. Marriott, 11 March 1996. SAIAB 75826, 5 unsexed, 53.1–60.2 mm SL, Rondegat River, Olifants System, South Africa, -32.37333297, 19.0602779388, collected by R. Bills, 18 April 2005. SAIAB 75783, 3 unsexed, 49.7–58.6 mm SL, Algeria below weir, Rondegat River, Olifants System, South Africa, -32.37333297, 19.0602779388, collected by R. Bills, 13 September 2004. SAIAB 58324, 5 unsexed, 54.4–61.8 mm SL, below forestry camp, Rondegat River, Olifants System, South Africa, -32.35139846, 19.0333003998, collected by R. Bills and D. Naran, 05 February 1998.

Pseudobarbus quathlambae (Barnard, 1938): SAIAB 189215, 3 unsexed, 31.5–49.8 mm SL, Himeville, Natal, Mkhomazi River system, South Africa, -29.72078, 29.51226, collected by M. Copeland, unknown date. SAIAB 131399, 7 unsexed, 54.0–76.4 mm SL, Jordane River, Lesotho, -29.432, 28.07805, collected by K.J. Meyer, 26 May 1986. SAIAB 25491, 4 unsexed, 59.5–76.1 mm SL, Jordane River, Lesotho, -29.39500045, 28.0424995422, collected by K.J. Meyer, 27 October 1985. SAIAB 131400, 4 unsexed, 69.1–86.4 mm SL, Bokong River, Lesotho, -29.27027, 28.126, collected by K.J. Meyer, 24 May 1986. SAIAB 29001, 6 unsexed, 59.3–79.5 mm SL, Sani River, Lesotho, -29.56083297, 29.2652778625, collected by P.H. Skelton, 22 September 1988. SAIAB 63417, 4 unsexed, 61.6–73.3 mm SL, Tsoelikane Falls, Tsoelikana River, Orange System, Lesotho, -29.89749908, 29.1205997467, collected by R. Bills & J. Rall, 02 October 2000. SAIAB 63409, 2 unsexed, 76.1–76.5 mm SL, headwaters of Moremoholo River, Orange System, Lesotho, -29.12470054, 29.3271999359, collected by R. Bills & J. Rall, 29 September 2000. SAIAB 63408, 2 unsexed, 65.6–65.7 mm SL, Senqu River, Orange System, Lesotho, -28.92280006, 29.0242004395, collected by R. Bills & J. Rall, 29 September 2000. SAIAB 63408, 2 unsexed, 81.1–90.4 mm SL, Matsoku River, Orange System, Lesotho, -29.2838993, 28.5531005859, collected by M. Nthimo, 07 February 2000.

Pseudobarbus senticeps (Smith, 1936): SAIAB 304 (holotype), male, 65.7 mm SL, Assegaaibosch River, Krom River system, South Africa. SAIAB 200302,

9 unsexed, 23–83 mm SL, Assegaaibos River, Krom River system, South Africa, -33.9452778, 24.3139167, collected by R. Bills, V. Bills and D. Naran, 12 August 2014. SAIAB 121815 (formerly AMG 2651), 29 unsexed, 45–75 mm SL, Assegaaibosch River, South Africa, -33.9413889, 24.3188889, Krom River system, collected by P.H. Skelton and J. Stephenson, 20 January 1975.

Pseudobarbus skeltoni Chakona & Swartz, 2013: SAIAB 187243, holotype, male, 158.2 mm SL, Riviersonderend River upstream of Theewaterskloof Dam, Breede River system, South Africa, -34.0623055556, 19.0705, collected by A. Chakona & J. Merron, 5 December 2009. SAIAB 187244, BMNH 2012.9.17.1, USNM 408375, same data as for holotype. SAIAB 187241, 5 specimens, 96–111 mm SL, Krom River, tributary of the Molenaars River, Breede River system, South Africa, -33.7227, 19.11294, collected by A. Chakona, J. Merron & M. Jordaan, 3 December 2009. SAIAB 187242, 2 specimens, 57–58 mm SL, collected 200 m upstream of locality for SAIAB 187241, same date and collectors. SAIAB 122627, 4 specimens, Wit River (Bainskloof), Breede River system, South Africa, collected by P.H. Skelton and P.H. Greenwood, 14 October 1975. SAIAB 187238, 2 specimens, 79–136 mm SL, Wit River (Bainskloof), Breede River system, South Africa, collected by F.L. Farquharson, 3 April 1967.

Pseudobarbus swartzi Chakona & Skelton, 2017: SAIAB 203792 (holotype), male, 80.9 mm SL, tributary of the Wabooms, Gamtoos River system, South Africa, -33.8639772, 23.82633, collected by A. Chakona, B. Motshegoa, N. Mazungula, W. Kadye and R. Smith, 21 January 2015. SAIAB 203793, 9 unsexed, 35.4–76.0 mm SL, Tributary of the Wabooms, Gamtoos River system, South Africa, -33.8639772, 23.8263, collected by A. Chakona, B. Motshegoa, N. Mazungula, W. Kadye and R. Smith, 21 January 2015. MRAC 2016-032-P-0001-0004 (Field no.: AC16AL02), 4 unsexed, 50.2–61.4 mm SL, main tributary of the Louterwater River, -33.8333611, 23.6373056, Gamtoos River system, South Africa, collected by A. Chakona, S. Reddy and R. Smith, 18 January 2016. SAIAB 203772, 10 specimens, unsexed, 25.5–57.9 mm SL, Western Tributary of the Louterwater River, -33.825750, 23.6310, Gamtoos River system, South Africa, collected by A. Chakona, S. Reddy and R. Smith, 18 January 2016. SAIAB 203779, 6 specimens, unsexed, 32–64.8 mm SL, Main Tributary of the Louterwater River, -33.8333611, 23.6373056, Gamtoos River system, South Africa, same collectors and date as SAIAB 203772. SAIAB 203787, 34 specimens, unsexed, 18.2–86.7 mm SL, upper Dwars River, -33.6534, 23.7539722, Gamtoos River system, South Africa, same collectors and date as SAIAB 203772. SAIAB 203786, 17 specimens, unsexed, 34.8–64.9 mm SL, Klein River at Kouga Wilderness, -33.7112, 23.844083, Gamtoos River system, South Africa, same collectors as SAIAB 203772, 19 January 2016. SAIAB 203789, 8 specimens, unsexed, 47.8–70.2 mm SL, Braam River, -33.7135278, 23.8465833, Gamtoos River system, South Africa, same collectors as SAIAB 203772, 19 January 2016. SAIAB 203788, 13 specimens, unsexed, 17.9–63.3 mm SL, Diep River, -33.7541944, 24.0812500, Gamtoos River system, South Africa, collected by A. Chakona and R. Smith, 20 January 2016. SAIAB 203781, 45 specimens, unsexed, 14.7–53.8 mm SL, Upper Kansenkei River, -33.7296667, 24.5545833, Gamtoos River system, South Africa, same date and collectors as SAIAB 203788. SAIAB 203774, 10 specimens unsexed, 25.5–57.9 mm SL, Wit River, -33.65383, 24.51605, Gamtoos River system, South Africa, collected by A. Chakona and B. Motshegoa, 7 March 2016. SAIAB 203780, 5 specimens unsexed, 24.6–58.8 mm SL, Lourie River, -33.8506944, 25.0388194, Gamtoos River system, South Africa, collected by A. Chakona and B. Motshegoa, 7 March 2016. SAIAB 120538, 70 unsexed, Kouga Dam, Gamtoos River system, South Africa, -33.6, 24.516, collected by F. Farquharson, 6 July 1967. SAIAB 120539, 70 unsexed, same locality and collector as SAIAB 120538.

Pseudobarbus verloreni Chakona, Swartz & Skelton, 2014: SAIAB 186092, holotype, 70.8 mm SL, 20 m upstream from railway at the Het Kruis bridge on R365, Verlorenvlei River system, South Africa, -32.60179, 18.75039, collected by E. Swartz & W. Bronaugh, 13 March 2012. SAIAB 192542, paratypes, 3 specimens, 53.3–70.8 mm SL, same data as for holotype. SAIAB 59808, paratypes, 10 specimens, 40.1–46.9 mm SL, Verlorenvlei River system, South Africa, -32.74560165, 18.81780052, collected by R. Bills & D. Naran, 22 January 1999. BMNH 2014.2.26.1-2 (2 specimens, 52.8–58.2 mm SL), USNM427302 (2 specimens, 53.4–56.8 mm SL), and MRACB4-03-P-1-2 (2 specimens, 53.0–54.5 mm SL), paratypes, same data and collectors as SAIAB 59808. SAIAB 121038, paratypes, 10 specimens, 34.0–68.0 mm SL, Verlorenvlei River system, South Africa, collected by P. Skelton, C. Gaigher & D. Heard, 1973. SAIAB 121039, paratypes, 17 specimens, 41–57 mm SL, Kruis River, Verlorenvlei River system, South Africa, collected by P. Skelton, C. Gaigher & D. Heard, 1973.

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